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Linking habitat quality to population dynamics for conservation decision making

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Linking habitat quality to population dynamics for conservation decision making

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Table of contents

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Editorial: Linking habitat quality to population dynamics for conservation decision making

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Editorial on the Research Topic
Linking habitat quality to population dynamics for conservation decision making

Introduction

Natural and anthropogenic factors alter habitats so that trends, random sampling, or single snapshots of habitat conditions often do not predict future species abundance (Kunegel-Lion et al., 2022; Conquet et al., 2023). Habitat dynamics are measured at different spatial scales (e.g., landscape, management units, patch, territory) and are asynchronous and driven by climate change, disturbances, invasive species, and habitat management.

Endangered species recovery plans and species status assessments have requirements to address time to population recovery, but they often do not adequately address habitat dynamics and factors that led to endangerment (Auld and Keith, 2009; Shirey et al., 2022). Understanding how habitat dynamics influence population dynamics is necessary for making sound conservation decisions.

Examples across a range of species, habitat and actions are important to facilitate decision making (Runge, 2011). From literature reviews, we found 160 individuals as potential authors and invited them to contribute, leading to 9 manuscripts. Below we summarize these studies and related literature to describe improvements to support conservation decision making.

Decision making and adaptive management

Nichols et al. introduced Structured Decision Making (SDM) and Adaptive Resource Management (ARM) topics used in natural resource management and a framework to combine population and habitat variables in a statistical likelihood approach. Our view of habitat conditions was broad, for example including human disturbance as a factor that altered habitat suitability (e.g., Martin et al., 2011). Peterson and Duarte used integrated models to prioritize salmon habitat restoration in perennial versus ephemeral habitats depending on whether essential suitable perennial habitat was already present, but ephemeral habitats could produce greater salmon growth and survival during high-water years.

Eaton et al. use a portfolio of strategies for an endangered Puerto Rican frog where uncertainties could result in conservation failure due to climate changes, so that several strategies might be best. Stantial et al. describe the initial stage of the experimentalist school of adaptive management, emphasizing stakeholder involvement, shared understanding, and plans for experimentation that eventually could reduce the uncertainty around the use of prescribed fire for salt marsh bird species.

Linking separate models

Early work on linking habitat and population dynamics used the Landis Forest succession models (e.g., Akçakaya, 2001; He, 2009), which led to other approaches such as state transition models (e.g., Raphael et al., 2013). Later metamodeling approaches used separate disease, predator-prey dynamics, and habitat dynamics models to pass information to population viability analysis (PVA) models (Lacy et al., 2013). In this Research Topic, Lacy et al. provide an example linking a predator (polar bears), prey (pinnipeds), and habitat change (declining Arctic sea ice).

Lacy et al. provide a PVA that includes habitat dynamics at the territory scale exploring both habitat and population management options to provide for sustainable Florida scrub-jay populations in a fragmented landscape. This modeling relied on long-term research of populations and habitat dynamics and learning from ARM that linked habitat, population data, and decision making, and brought stakeholders, biologists, and managers together. Forero-Sanchez et al. use a PVA of an endangered tamarin with a plant-based energetic model to estimate carrying capacity for subpopulations, incorporating climate change, fire risk, and habitat connectivity through forest corridors to estimate inter-population dispersal and metapopulation persistence.

Further complications such as connecting different geographic areas and multispecies planning

Bohnett et al. show how a combination of connectivity models for focal species with complementary and opposing habitat requirements can better inform landscape design to prioritize conservation areas in landscapes with rapid human development. Schumaker shows a landcover map and movement simulator for an endangered butterfly to explore the concepts and mechanics behind a novel connectivity assessment methodology.

Integrated population models (IPM) can combine population data and habitat to incorporate habitat and population dynamics in both breeding and wintering areas (Osnas et al., 2021). Information about many species of conservation concern with different requirements has been integrated into IPMs to make decisions about fire management (Conlisk et al., 2015).

Conclusions and actions for a sustainable future

The examples above demonstrate that a broad variety of approaches are available for modeling ecosystems and species to serve conservation decision-making, providing a large toolbox that includes both canned and investigator-adapted coding. Both modeling and monitoring are generally needed to resolve uncertainties (Armstrong and Reynolds 2012, Converse and Armstrong 2016). Monitoring provides fantastic opportunities for learning and is often a regulatory requirement used in negotiation, but its implementation to make better decisions is often not well developed (Yoccoz et al., 2001, Nichols and Williams 2006, Nichols and Armstrong 2012). We suggest monitoring should address the 4 major reasons for monitoring to support decision-making described in this volume Nichols et al. We suggest applications increase collaboration among population biologists, geneticists, field biologist, managers, stakeholders, and habitat modeling experts.

Author contributions

DB: Writing – original draft, Writing – review & editing. DA: Writing – original draft, Writing – review & editing. JN: Writing – original draft, Writing – review & editing. RL: Writing – original draft, Writing – review & editing.

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An evaluation of tradeoffs in restoring ephemeral vs. perennial habitats to conserve animal populations

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Introduction: Habitat loss and degradation pose significant threats to global fish and wildlife populations, prompting substantial investments in habitat creation and restoration efforts. Not all habitats provide equal benefits, leading to challenges in prioritizing restoration actions. For example, juvenile anadromous salmonids require high quality rearing aquatic habitats to achieve the physiological requirements needed to successfully migrate to the ocean. However, there are profound disagreements among anadromous salmon restoration managers whether it is best to focus efforts on restoring in-channel habitats that are available for the entire rearing period or floodplain habitats that, while facilitating greater growth and survival than in-channel habitats, are only available for a few weeks at a time and are typically only activated every two-to-three years.

Methods: We used an existing fall-run Chinook salmon decision-support model to evaluate under what conditions floodplain restoration would provide greater benefits than in-channel habitat restoration. The simulations included a wide range of floodplain inundation frequencies and durations and floodplain benefits in the form of increased survival and growth relative to in-channel habitats.

Results: The simulations results indicated that in-channel habitat restoration was always the best habitat restoration action when there was no existing in-channel habitat despite simulating a wide range of flood frequency, duration, and growth and survival benefits. Floodplain restoration was generally best when there was sufficient in-channel habitat available to successfully rear most of the juveniles produced by the returning adult salmon.

Discussion: We hypothesize that in-channel and floodplain habitats have different roles in salmon population maintenance with in-channel habitats regulating the overall population size and floodplains acting as recurrent resource pulses. Our study provides a quantitative framework to evaluate the benefit of these two habitat types and provides generalizable rulesets that can be used by managers when implementing habitat restoration strategies for species that inhabit both in-channel and floodplain habitats.

KEYWORDS

Chinook salmon, Central Valley, pulsed resource, decision model, simulation

1 Introduction

Habitat loss and degradation are among the primary threats to many fish and wildlife populations across the globe. In response, managers have invested considerable resources into habitat creation or restoration efforts to conserve animal populations (BenDor et al., 2015; Höhl et al., 2020; Bodin et al., 2022). Not all habitats provide the same benefits to the species they are intended to support. In some cases, the relative benefits are more easily distinguishable, such as habitats to support reproduction (i.e., spawning or nesting habitats) versus habitat to support foraging (i.e., rearing and foraging habitats). However, the relative benefits are much more difficult to ascertain when different habitat types are intended to support the same life stage or activity, but the quality and availability of the habitats varies. For example, juvenile anadromous salmonids require perennial in-channel aquatic habitats to rear to achieve the physiological requirements needed to successfully migrate to the ocean (Honea et al., 2009; Bourret et al., 2016). Although floodplain habitats serve similar functions as their in-channel counterparts, these habitats are also widely documented to facilitate increased somatic growth in salmonids due to an increase in food availability (Jeffres et al., 2008; Opperman et al., 2017). Importantly, these increased somatic growth rates have been linked to increased survival of juvenile salmonids. Therefore, floodplain habitats provide important benefits over in-channel habitats. However, floodplain habitats are ephemeral, where they are often only available every two-to-three years and are typically only activated for a few weeks at a time (Williams et al., 2009).

Given the often-limited resources available to invest into habitat restoration efforts, managers are regularly assigned the difficult task of prioritizing which habitat types to invest in (and where) to promote healthy salmonid populations. To help address these challenges, we developed quantitative decision-support models (DSMs) to evaluate alternative habitat restoration actions for salmonids in the Central Valley of California, U.S.A (Peterson and Duarte, 2020). These DSMs were used by a stakeholder group, the Science Integration Team (SIT), as they participated in the structured decision-making process to help inform the development of a five-year habitat restoration strategy for the Central Valley Project Improvement Act (CVPIA) Fisheries Program (USBR and USFWS, 2020). At the time, the DSMs indicated that in most cases increasing the amounts of perennial in-channel habitat led to substantially increased fish abundances when compared to scenarios that increased the availability of ephemeral floodplain habitats. By extension, the five-year habitat restoration strategy prioritized the creation of perennial in-channel habitats over ephemeral floodplain habitats to restore anadromous salmon populations.

As they continue to participate in the structured decision-making process, the SIT recently reinitiated the conversations that will likely inform the development of the next five-year CVPIA Fisheries Program restoration strategy aimed at promoting salmonid populations in the region. Over the past five years, the SIT has gathered improved information on current conditions in the Central Valley, and we have subsequently revised the DSMs to more accurately capture the best available science and hypotheses on system dynamics in the region. However, there is significant disagreement among stakeholders, with some advocating for the restoration of ephemeral floodplain habitats as the most effective means to restore anadromous salmon populations despite previous model runs. Much of this conflict arises from the uncertainty regarding the greater somatic growth and survival benefits to juvenile salmonids that use floodplain habitats and a belief among some SIT members that created/restored floodplains can be engineered to increase the frequency of inundation over more natural floodplain habitats.

Herein, we focused our study on fall-run Chinook salmon (*Oncorhynchus tshawytscha*) because they occur in all of the natal tributaries in the DSMs and modified this DSM to more explicitly evaluate tradeoffs in restoring ephemeral floodplain habitats versus perennial in-channel habitats to promote salmonid populations. Similar to Peterson and Duarte (2020), we focused on the modules that simulate juvenile salmonids as they rear in freshwater environments before making their migration to oceanic waters. Our goal of this study was to use the DSM to evaluate under what conditions ephemeral floodplain habitats provide greater benefits than perennial in-channel habitats when the objective is to maximize the number of juvenile salmonids that return as adults. Thus, we considered a broad range of possible environmental conditions and effect sizes within our evaluation. Given our previous evaluations of these habitat types, we hypothesized that floodplain habitats would likely only be considered more beneficial than in-channel habitats when the survival of juvenile fish rearing in in-channel habitats was low and the availability of existing rearing habitat (either in-channel or floodplain) during the early outmigration window (when floodplains are typically activated) was relatively limited.

2 Methods

2.1 Restoration area

The eponymously named California Central Valley is situated between the Coast Ranges and the Sierra Nevada mountain range of California, USA. It is made up primarily of two watersheds, the Sacramento River to the north and the San Joaquin River to the south. The Central Valley climate is characterized by Mediterranean-like conditions, with hot, dry summers and mild, wet winters (Deitch et al., 2017). Streamflows in the Central Valley are derived principally from the snowpack in the Sierra Nevada and are greatest in the winter and lowest in the summer. The spatial extent of the restoration area includes the Sacramento and San Joaquin Rivers and their tributaries and the major tributaries that drain into the central portion of the Sacramento-San Joaquin Delta. Candidate restoration areas included only stream segments and adjacent riparian areas downstream of major obstructions to upstream migration, such as Shasta Dam on the Sacramento River. The spatial grain of the restoration area was individual tributaries, except the San Joaquin River below the Merced River was the only section included in these DSMs, and the mainstem Sacramento River was subdivided into four sections.

2.2 Model overview

The Chinook salmon DSMs are thoroughly documented in Peterson and Duarte (2020) and available at https://github.com/CVPIA-OSC/fallRunDSM. We briefly described them here. These stochastic DSMs tracked the number of juvenile salmon in four size groups: small, < 42 mm total length; medium, 42–72 mm; large, 72–110 mm; and very large, > 110 mm and the returning adult stage. Transitions between stages were estimated using survival and growth parameters that varied with simulation and represented conditions in the natal tributaries, migratory corridors, delta, and ocean. The DSMs originally operated on a monthly time step but we adjusted the parameters for this study to coincide with a weekly time step to facilitate evaluations of different floodplain inundation durations. Again, we focused the evaluation on fall-run Chinook salmon because they occur in all of the natal tributaries in the DSMs. Therefore, juvenile rearing occurred over a 30-week period from January to August. All simulation modeling was conducted using R statistical software v 4.3.2, “Eye Holes” (R Core Team, 2023).

The DSM simulations began with 10,000 adults in a natal tributary. Because we were primarily focused on identifying the relative benefits of juvenile rearing habitat restoration (i.e., in-channel and floodplain habitats), we assumed that there was sufficient spawning habitat for all spawning adult salmon in our evaluations. The number of small-sized juvenile salmon produced was estimated as a function of the number of spawning adults, adult prespawn survival, adult sex ratio, female fecundity, and egg-to-fry survival (Table 1; Figure 1). Juvenile salmon reared in their natal tributaries until habitat capacity was exceeded and capacity was a function of the number of juvenile fish and fish body size (i.e., juvenile territory size; Table 1). Juvenile salmon habitat use and movement out of a natal tributary were modeled using a habitat and body sized-based ruleset. For each weekly time step, juvenile fish used all available habitat with larger fish occupying available habitat first. Floodplain habitats were filled first when they were inundated/activated; when capacity was exceeded in floodplains, the remaining fish were assigned to in-channel habitats until in-channel habitat capacity was exceeded. Excess fish that were not assigned to habitats (i.e., habitat capacity was exceeded) left the natal tributary. Fish that remained in a natal tributary survived and grew as a function of habitat type and body size that varied with simulation scenario, as detailed below. Fish that transitioned to the very large size class left the natal tributary the next time step. Similarly, all juvenile salmon that remained in their natal tributaries at the start of week 30 left the natal tributary. Juveniles leaving their natal tributaries migrated to the delta, the bay, then the ocean and survived as a function of time and migration distance that varied with simulation scenario. Juveniles entering the ocean survived as a function of fish body size and the timing of ocean entry relative to ocean productivity transition (Satterthwaite et al., 2014). This ocean entry survival estimates the probability that a juvenile salmon entering the ocean successfully returns to freshwater as an adult (Supplementary Information). We defined these fish as adult equivalents and used this measure to quantify the relative benefits of perennial in-channel and ephemeral floodplain habitat restoration (Figure 1).

TABLE 1 Fall-run Chinook salmon (*Oncorhynchus tshawytscha*) decision-support model baseline parameters with (+/-) standard deviations and scenario specific values used in evaluation of the relative value of restoring in-channel and floodplain juvenile salmon habitats.

Parameters	Simulated values
Baseline model	
Adult prespawn survival	0.85 +/- 0.05
Female fecundity	5522 +/- 74
Adult sex ratio	0.50 +/-0.1
Egg-to-fry survival	0.51 +/- 0.05
In-channel habitat growth rate (mm per week)	3.5 +/- 1.2
Juvenile territory size (m^2) for small, medium, and large sizes	0.054, 0.145, 0.485
Scenario-specific	
In-channel habitat survival of small juveniles	0.74, 0.84, 0.92
Change in survival with body size (log-odds)	0.01,0.02, 0.03
Increase in survival in floodplain habitats (log-odds)	0.5, 1.0, 1.5
Floodplain habitat growth rate (mm per week)	7.0, 10.5, 14
Flood frequency (annual probability of flood)	0.25, 0.50, 0.75, 1.0
Flood duration (weeks)	1, 2, 3, 4
Current in-channel habitat availability (m^2 per adult spawner)	0, 100, 300
Current floodplain habitat availability (m^2 per adult spawner)	0, 100, 300
Floodplain habitat addition multiplier	1, 5, 10
Subsidized juvenile growth rate in in-channel habitats (mm/day)	5.25, 7.0

2.3 Evaluation scenarios

Again, our main goal was to identify the conditions whereby floodplain habitat restoration would result in a greater number of expected adult equivalents than in-channel habitat restoration. Previous sensitivity analyses of the DSMs indicated that the rankings of best Chinook salmon habitat restoration actions were most sensitive to juvenile survival and growth rate and habitat availability (Peterson and Duarte, 2020). Therefore, we identified low, medium, and high weekly survival rates of the small size group based on estimated natal rearing survival in Central Valley tributaries (Table 1). Floodplain habitats are believed to have higher survival and growth rates, so we evaluated floodplain survival at rates 1.6, 2.7, and 4.5 times greater and growth rates 2, 3, and 4 times greater than in-channel habitats (Table 1). The smallest of these growth and survival increases in floodplain

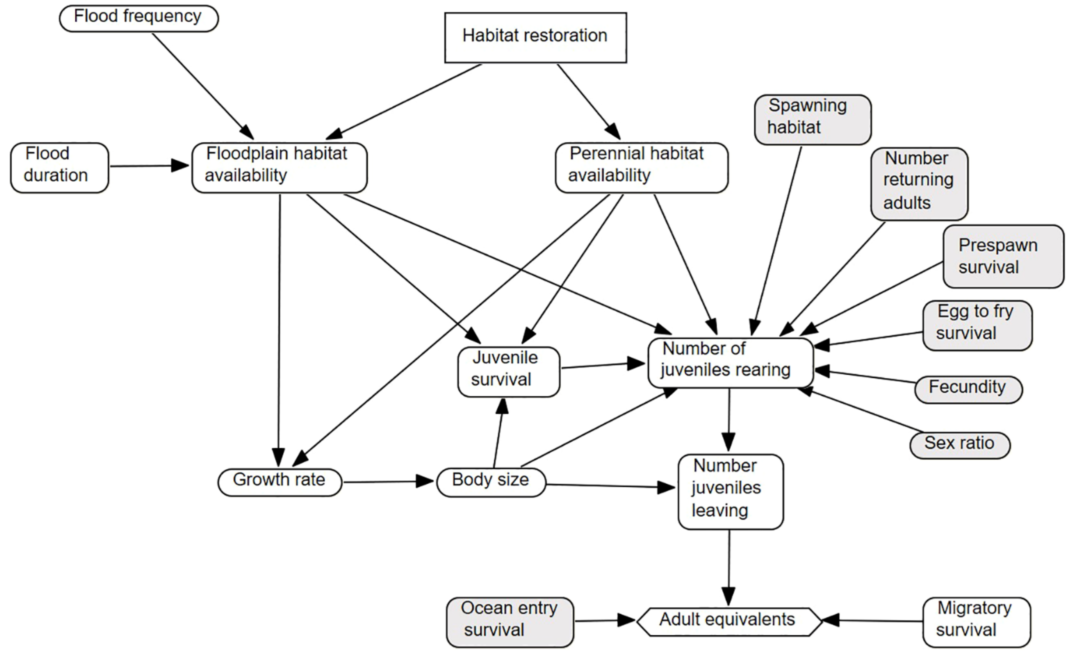

FIGURE 1
Influence diagram representing the fall-run Chinook salmon (*Oncorhynchus tshawytscha*) decision-support model for evaluating the relative benefits of restoring in-channel and floodplain habitats. Shaded components were the same across simulation scenarios.

habitats were used in the DSM for informing the development of the five-year habitat restoration strategy for the CVPIA Fisheries Program (Peterson and Duarte, 2020). The greater sizes attained by fishes rearing in floodplain habitats may impart a survival benefit after the floods recede so we identified three increasing levels of body size effects on survival in rearing juvenile salmon (Table 1). Overbank flows required to inundate floodplains typically occur once every other year (Wolman and Leopold, 1957) but floodplain activation flows (i.e., the smallest 7-d flows that initiate ecological processes in the floodplain) occur two of every three years (Williams et al., 2009). We therefore evaluated the effect of flood frequency at four levels: one lower and two higher than overbank and floodplain activation flows (Table 1). Floodplains can be activated for intervals ranging from days to weeks, but generally require about 7 d to initiate the ecological processes that produce food subsidies for fish (Williams et al., 2009). We evaluated the effects of floodplain duration at four levels ranging from 1 to 4 weeks (Table 1). Existing habitat availability was also simulated at four levels of availability that represented no (zero) habitat, medium, and high levels of habitat availability for both in-channel and floodplain habitats (Table 1). The high in-channel habitat availability value is approximately the value when juvenile rearing habitat is no longer limiting under average conditions in the Central Valley tributaries (e.g., state-dependent policy plots in Peterson and Duarte, 2020). Based on the CVPIA Fisheries Program internal records, juvenile rearing habitat restoration creates, on average, 0.8 ha of in-channel or floodplain habitat in the DSM under the assumption that both actions require similar expenditure of resources to complete. To evaluate circumstances when similar effort can produce more floodplain habitat, we evaluated the relative benefits of floodplain restoration for three multiples applied to 0.8 ha: one (equal to in-channel habitat), five, and ten times (Table 1). Note that these restoration area scenarios can also be interpreted as greater fish holding capacity for the same unit area restored.

Perennial in-channel habitat availability fluctuated systematically through time in the natal tributaries in Central Valley based on flow regimes and the fluctuations can affect the efficacy of habitat restoration actions (Peterson and Duarte, 2020). Therefore, we used three functions to simulate situations representing increasing, decreasing, and stable habitat availability through time (Figure 2). The probability a juvenile salmon that was migrating to the ocean survived (outmigrant survival) also varied among natal tributaries due to their distance from the ocean and location. To incorporate these effects, we simulated under four outmigrant survival patterns (Figure 2) that represented the typical patterns in the Central Valley DSMs.

Finally, floodplains are also believed to provide a food subsidy to fishes that are not using the floodplain during inundation (i.e., fish rearing in adjacent in-channel habitats), and there is some evidence to support this hypothesis (Górski et al., 2013; Farly et al., 2019). However, the magnitude and extent of the food subsidy are largely uncertain. To incorporate this uncertainty, in a *post hoc* evaluation we applied a food subsidy under two assumptions of the spatial extent. The first applied the food subsidy to all juvenile salmon rearing in the in-channel habitat within the tributary during floodplain inundation. The second applied the subsidy to a portion of fish rearing the adjacent in-channel habitats that equaled the fish rearing capacity of the floodplain habitat in the tributary. Thus, the extent of the subsidy under the second assumption was

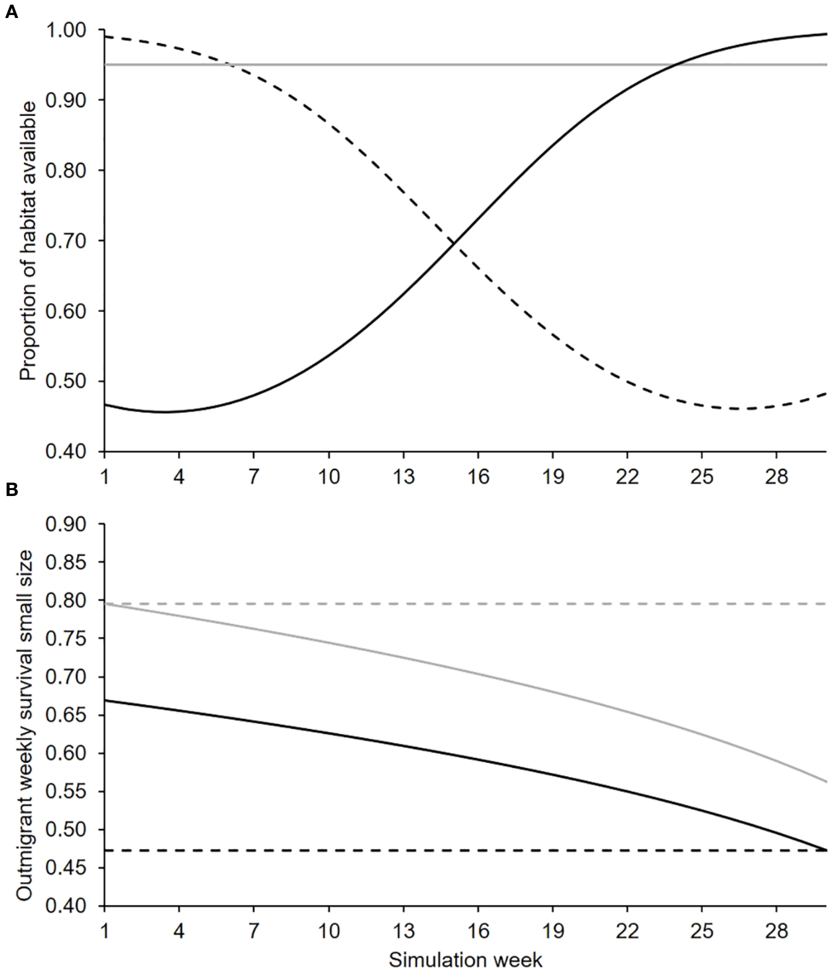

FIGURE 2
Change in in-channel habitat availability across the 30-week simulation **(A)** under decreasing (broken line), constant (solid gray), and increasing (solid black) trends and **(B)** outmigrant survival under low (black) and high (gray) survival with constant (broken line) and decreasing trends (solid).

proportional to the amount of floodplain in a tributary. We also evaluated two growth rates for food subsidized fish at 1.5 and 2 times that of baseline in-channel habitat rates (Table 1).

2.4 Scenario simulation

We conducted two sets of simulations. The first set of simulations focused on evaluating the relative benefits of in-channel and floodplain habitat restoration without floodplain food subsidies. The second set of simulations examined the same tradeoffs, but included the additional benefits of food subsidies. For both sets of simulations, the expected number of adult equivalent salmon was estimated under three candidate actions: no restoration, 0.8 ha in-channel habitat restoration, and floodplain habitat restoration that varied with scenario (i.e., 0.8–8.0 ha). During the simulations, stochasticity was imposed by drawing parameters from statistical distributions with means and standard deviations in Table 1. The flood frequency was simulated using a Bernoulli distribution and the week the flood event was initiated was randomly assigned to one of the first 12 weeks of the year with equal probability (i.e., a unform distribution). The number of fish that transitioned from one state to another (e.g., surviving week to week) were modeled using a binomial distribution. The first set of simulations evaluated all combinations of scenario specific parameters (without the subsidy), the three in-channel habitat dynamics trends, and the four outmigrant survival patterns. The food subsidy simulations also included all combinations of the scenario specific values except for current in-channel habitat availability that was fixed at the middle value (100 m^2 per adult spawner), habitat dynamics was fixed at constant, juvenile survival was evaluated for the two lowest values (Table 1), and the outmigrant survival pattern was fixed at the high and decreasing pattern (Figure 2). We simulated 10,000 replicates for each scenario and estimated the mean number of adult equivalent salmon. For each combination, we considered the best restoration action to be the action that resulted in the greatest number of adult equivalent salmon.

The large number of simulation combinations and potentially interacting factors would make it difficult to identify the conditions that floodplain habitat restoration was preferable to in-channel habitat restoration. Therefore, we created binary indicators (0,1) for observations that had no action as the best restoration action and another indicator for observations when floodplain habitat restoration was the best restoration action. We then used logistic regression to fit all combinations of scenario parameters and two-way interactions and selected the best fitting model using Akaike's Information Criteria (AIC; Akaike, 1973) with the small-sample bias adjustment (AICc; Hurvich and Tsai, 1989). The no food subsidy and food subsidy simulations were analyzed separately. Given the scenarios were simulated using discrete values, we treated all covariates as factor variables in our analyses. The no action regression models were fit using all of the scenarios, whereas the floodplain action regression models were fit to simulation data that excluded the combinations when no action was the best alternative. Thus, predictions under the floodplain restoration action should be interpreted as the probability that floodplain habitat restoration is the best restoration action relative to in-channel habitat restoration.

3 Results

Perennial in-channel habitat restoration was the best restoration action for a vast majority of simulation combinations (73%) compared to no action (13%) and floodplain restoration (14%) under the no subsidy scenarios. Similarly, in-channel habitat restoration was best restoration action in 83% of food subsidy simulations followed by floodplain restoration (14%), and no action (3%). On average, 295 and 215 more adult equivalent salmon were produced relative to no action when in-channel and floodplain restoration, respectively were the best restoration action. When current in-channel habitat availability was zero, in-channel habitat restoration was always the best restoration action. Therefore, simulations with zero current in-channel habitat availability were removed from the data prior to logistic regression model fitting to avoid quasi-complete separation.

The best fitting no restoration action model fit to the simulated no subsidy data contained all but two simulation parameters, flood frequency and outmigrant survival, and 103 two-way interactions (Supplementary Material). Again, no action was never selected when there was zero current in-channel habitat availability. The main effects parameters suggested that seasonal change in in-channel habitat availability and current in-channel and floodplain habitat availability had the greatest influence on the probability that no action was the best restoration action. The interactions suggested that those factors in combination with in-channel habitat survival of juveniles and change in survival with body size largely drove the no action decision. Plots of predicted probabilities for combinations of simulation parameters suggested that the probability that no action was the best was greatest when current in-channel and floodplain habitat availabilities were high (albeit there was a stronger and more consistent effect of current in-channel habitat availability), in-channel habitat survival of juveniles was high, and seasonal change in in-channel habitat availability was decreasing through the rearing period (Figure 3). However, probability that no action was the best when seasonal change in in-channel habitat availability was increasing tended to be higher when in-channel habitat was low.

The best fitting floodplain restoration action model fitted with the no subsidy data also contained most of the simulation parameters except the floodplain habitat addition multiplier and there were 129 two-way interactions (Supplementary Material). Similar to the no restoration action model, current in-channel and floodplain habitat availability, in-channel habitat survival of juveniles, and the change in survival with body size were the most influential factors on the probability that a floodplain restoration action was the best. Again, floodplain habitat restoration was never selected when there was zero current in-channel habitat availability. The predicted probability of floodplain was greatest when there was no current floodplain habitat availability, high in-channel habitat availability, and low in-channel habitat survival of juveniles (Figure 4). Floodplain restoration actions also tended to be best when the change in survival with body size was small and seasonal change in in-channel habitat availability was increasing through the

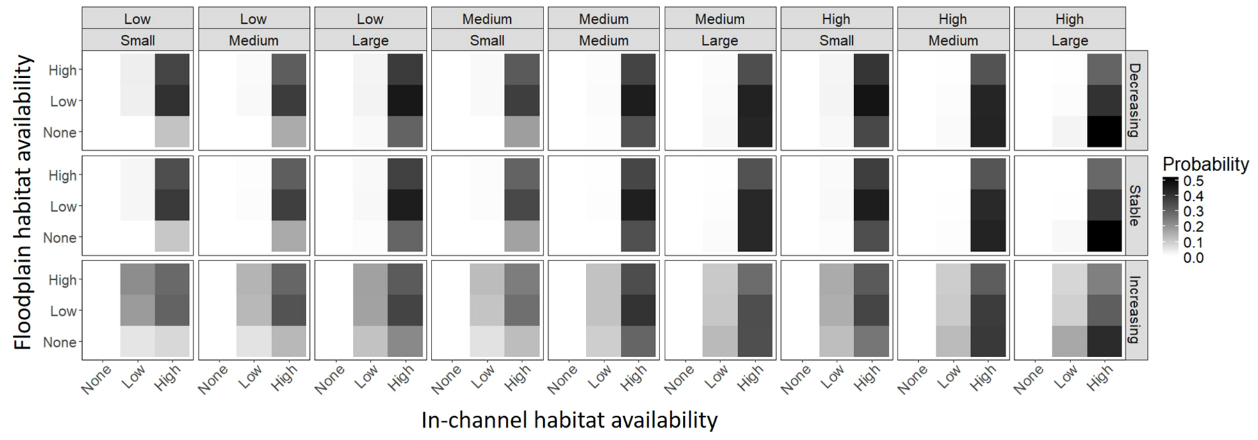

FIGURE 3
The mean predicted probability that no action was the best restoration action for combinations of juvenile in-channel habitat survival (top above), change in survival with body size (top inset), seasonal change in in-channel habitat availability (right), current in-channel habitat availability (bottom), and current floodplain habitat availability (left).

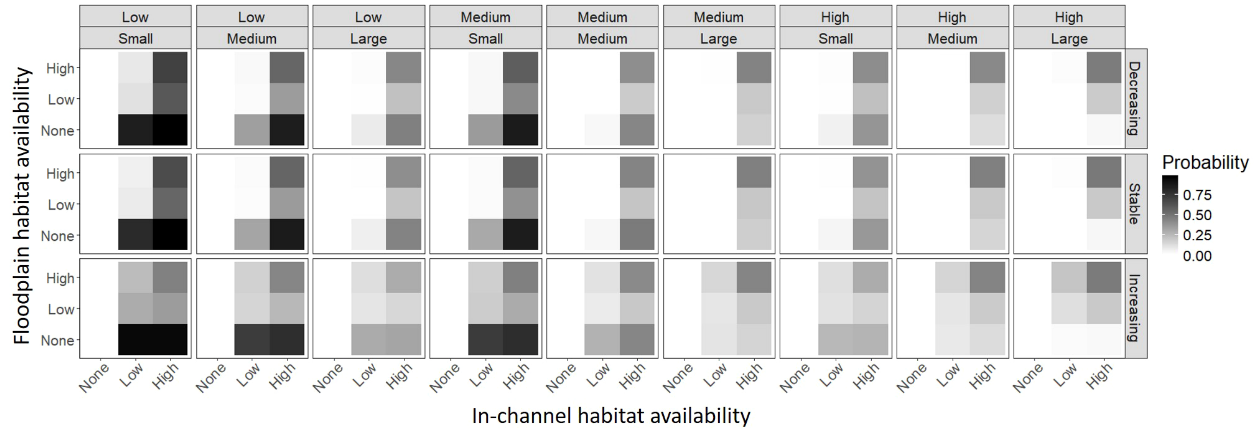

FIGURE 4
The mean predicted probability that floodplain restoration was the best restoration action (given the best restoration action was not "no action") for combinations of in-channel habitat survival of juveniles (top above), change in survival with body size (top inset), seasonal change in in-channel habitat availability (right), current in-channel habitat availability (bottom), and current floodplain habitat availability (left).

rearing period (Supplementary Material). Flood duration and the floodplain growth rate were also related to the probability that floodplain restoration action was best, but the effects were much lower than current floodplain habitat availability and flood frequency (Figure 5). Specifically, the probability floodplain restoration was the best action increased with lower current floodplain habitat availability.

Model selection of the floodplain food subsidy simulated data indicated similar relationships with current floodplain habitat availability, in-channel habitat survival of juveniles, and the change in survival with body size (Supplementary Material). However, it was also strongly influenced by the extent of the subsidy, flood frequency and duration, and the floodplain habitat addition multiplier. Under the subsidy simulations, the floodplain restoration action was generally the best restoration action when there was none-to-low current floodplain habitat availability and in-channel habitat survival of juveniles was low (Figure 6, top). The probability was also positively related to the extent of the floodplain food subsidy and flood frequency (Figure 6, bottom). Interestingly, the relationship with flood duration was not monotonic and appeared to peak at two-weeks.

4 Discussion

The fall-run Chinook salmon DSM used in this evaluation was a relatively simple model covering a portion of the salmon life cycle. Here, both habitat types served to hold and grow juvenile fish. However, fish in floodplain habitats had higher survival and growth rates compared to their counterparts rearing in in-channel habitat. Nonetheless, in-channel habitat restoration was always the best action when there was zero in-channel habitat available across a wide range of increased floodplain growth and survival benefits relative to those for fish rearing in in-channel habitat. Conversely, floodplain restoration tended to be the best restoration action when the existing in-channel habitat availability was near or exceeded the amount of in-channel habitat needed to rear most of the juveniles produced. This suggests that the two habitats have different, albeit interacting, roles with respect to salmon population maintenance. Because in-channel habitats are predictably available throughout the salmon rearing period and across years, we hypothesize that the availability of these perennial habitats largely determines the overall population size within a tributary (*sensu* Gibson, 1994). Floodplain habitats temporally increase the capacity of the system to support juvenile salmon, but they are typically not available all years and are not available throughout the entire 30-week rearing period. Thus, floodplain habitats can be viewed as a recurrent resource pulse that may alter the dynamics of fish populations (Holt, 2008).

Recurrent resource pulses can have a profound effect on population size and stability depending on how the resources affect population demographics. Mathematical evaluations of the effects of recurrent resource pulses suggest that pulses that temporarily increase population growth rate can increase population size (Cushing, 1987), whereas pulses that temporarily increase carrying capacity ultimately result in population decreases (Nisbet and Gurney, 1976) relative to stable environments. Experimental manipulations of captive populations exposed to recurrent resource pulses have shown that the pulses can maintain population sizes through increasing storage of energy (e.g., increased lipid reserves) that may act as a buffer during resource poor conditions (Costantino et al., 1998; Orland and Lawler, 2004). Such mechanisms are unlikely to occur in fall-run Chinook salmon, a semelparous species that spends a relatively small amount of their life-cycle in freshwater environments. Rather, the pulses increase habitat capacity, survival, and growth for the duration of the pulse resulting in more and larger individuals migrating to the ocean. The greater body size increases the survival in the ocean, depending on the timing of ocean entry (Satterthwaite et al., 2014). Thus, collectively floodplain habitats should result in greater number of returning adults in future years. Over multiple years, given Chinook salmon are known to have high fidelity to their natal tributaries, it seems plausible that increases in

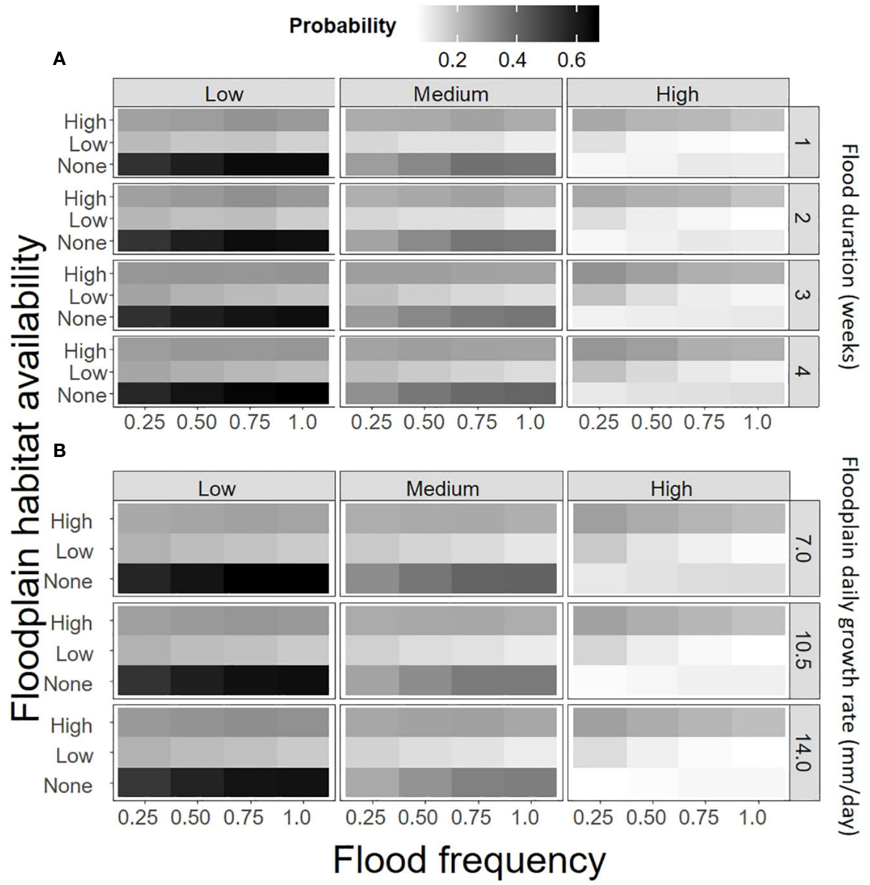

FIGURE 5
The mean predicted probability that floodplain restoration was the best restoration action (given the best restoration action was not "no action") for combinations of in-channel habitat survival of juveniles (top), flood frequency (bottom), and current floodplain habitat availability (left) for **(A)** flood duration and **(B)** floodplain growth rates.

returning adults associated with resource pulses could lead to the population exceeding capacity. If this occurs on the spawning grounds, this may lead to increased prespawn mortality. Although not ideal, it should be noted that one benefit of this potential outcome would be a temporary source of increased marine derived nutrients that would likely increase juvenile salmon body growth and condition downstream (Kaylor et al., 2020). If capacity is exceeded in the perennial in-channel habitats, however, this may lead to a deficit of rearing habitat resources (i.e., space and food), which may unintentionally lead to lower juvenile survival during rearing or juveniles outmigrating to the ocean too soon or at smaller body sizes (i.e., reduced ocean entry survival). To our knowledge, there have been no empirical assessments of the population-level effects of restoring resource pulses on salmon populations over multiple years. Without complete understanding of habitat deficits, it seems plausible that restoring ephemeral floodplain habitats rather than in-channel habitats may carry some additional risk.

The greater survival, growth, and increased carrying capacity associated with floodplain habitat restoration was usually not sufficient to produce a greater number of adult equivalent salmon when compared to in-channel habitat restoration. This pattern generally held even under simulations with growth subsidies for fish rearing in in-channel habitats and a flood frequency and duration of every year and four weeks, respectively. We believe that the near dominance of an in-channel habitat restoration action was primarily due to the duration and timing of the floodplain inundation and the timing of the juveniles entering the ocean. The floodplain growth rates we used in the simulations ranged from values similar to those observed in floodplains in the Central Valley (1 mm/day, Dudley et al., 2023) to twice that value. Nonetheless, this would only grow approximately 25% of fish in the small size group (on average) to very large size group over a four-week inundation period. Importantly, the habitat capacity for rearing juveniles decreased at the end of the flood event, resulting in a greater number of juveniles leaving the tributary either as very large fish outmigrating or as fish that were pushed downstream by larger rearing fish. This can translate into having a greater number of juvenile fish entering the ocean when they were too small and when ocean conditions were poor. This rationale is further supported by the higher probabilities of floodplain restoration being the best action when seasonal in-channel habitat availability increased through time (i.e., habitat dynamics increasing). The increased in-channel habitats were able to support some of the excess juveniles after the simulated floods ended. This suggests that the unpredictable and ephemeral nature of floodplain habitat

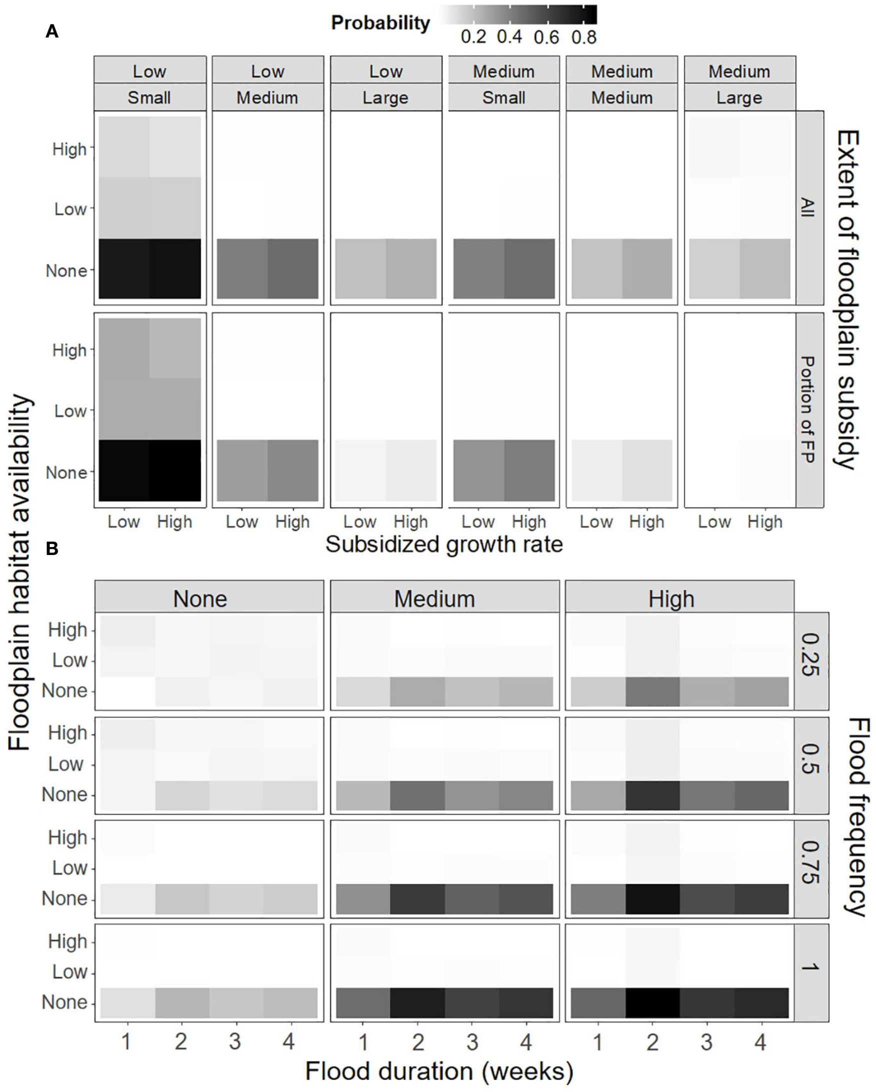

FIGURE 6
The mean predicted probability that floodplain restoration with a food subsidy was the best restoration action (given the best restoration action was not "no action") for combinations of **(A)** in-channel habitat survival of juveniles (top label), change in survival with body size (top inset label), the extent of the subsidy, subsidized growth rate and current floodplain habitat availability and **(B)** floodplain habitat addition multiplier (top label), flood frequency, flood duration and current floodplain habitat availability.

availability relative to in-channel habitats limit their value when in-channel habitat is limiting, particularly when in-channel habitat is relatively limited later in the rearing period. Thus, it makes logical sense that restoring floodplain habitats was never more advantageous when in-channel habitat availability is limiting.

Juvenile survival during rearing in freshwater also strongly affected the best restoration action. When existing in-channel habitat was insufficient for supporting most of the juveniles, floodplain habitat restoration tended to be the best restoration action when small juvenile survival was low and the effect of body size on survival was small (i.e., all juvenile fish tended to have low survival regardless of body size). This was particularly evident when there was no existing floodplain habitat. Juvenile Chinook salmon in the Sacramento River Basin rear in freshwater for 12 to 20 weeks, on average (Kjelson et al., 1982). Thus, survival of juveniles rearing in in-channel habitats under the low survival and small body size effect on survival for 12 and 20 weeks was on average 8% and 2% (respectively), whereas survival averaged 11% and 3% (respectively) for those juveniles that reared in floodplain habitats for two of the weeks. This small increase in survival may be sufficient to result in a greater number of adult equivalent salmon under the floodplain restoration action. However, floodplain habitat also holds rearing juvenile fish and grows them at a higher rate, which can alter the timing and size of fish leaving the rearing areas and entering the ocean. Simulated juvenile survival was less than 0.5% for any size juvenile that entered the ocean less than seven weeks after the ocean productivity transition occurred and was less than 1% for small juveniles at any time after the transition. Thus, we believe that the advantage of floodplain habitat restoration over in-channel habitat restoration under low juvenile survival was that it provided a higher survival environment that held and grew juvenile salmon early in the rearing period and provided an advantage when making the transition to the ocean environment.

Model assumptions undoubtedly affected our results. Sensitivity analysis of the full DSM indicated that the model was very sensitive to fish territory size and growth (Peterson and Duarte, 2020), two factors that govern habitat capacity and movement in the DSM. We incorporated these same mechanisms in this evaluation. Here, habitat capacity was inversely related to fish body size with capacity greater for smaller fish than larger fish and any fish that exceeded capacity left the natal tributary. Habitat capacity for juvenile salmonids is highly uncertain and can vary substantially in space and time (Beakes et al., 2014; See et al., 2021; Hall et al., 2023). Thus, unsurprisingly a variety of methods have been used to model juvenile salmon habitat capacity ranging from territory size (Grant and Kramer, 1990; this study), fixed numerical estimates based on published field observations (Hendrix et al., 2019), and density dependent functions calibrated using sample data (Perry et al., 2018). Similar to our DSM, many of these approaches postulate that fish that exceed habitat capacity leave the tributary and there is some empirical support for this mechanism (Connor et al., 2013). Were this the true mechanism governing habitat use by salmon in the natural environment, we expect our results to only differ qualitatively relative to the upper limit defining the amount of habitat sufficient to support most rearing juveniles (i.e., high existing in-channel habitat availability). However, there is also evidence of density dependent mortality in rearing juvenile salmon (Achord et al., 2003). This density dependent mechanism has been incorporated into some salmon life cycle models as a function of habitat capacity (Lee and Hyman, 1992; Greene and Beechie, 2004), so that fish died at a higher rate when capacity was exceeded rather than leaving the system. If this was the true density dependent response in the natural environment, we would expect our efforts to overestimate the benefits of floodplain habitat restoration because the individuals that experienced the benefits associated with a with floodplain inundation would remain in the tributary post-flooding and die at a higher rate rather than leave and potentially contribute to future adults. Within this evaluation, we only considered natal tributaries and assumed all fish that moved downstream were actively outmigrating to the ocean. In reality, fish leaving their natal tributaries have access to rearing habitats in the mainstem sections of the Sacramento and San Joaquin Rivers. We chose to make this simplifying assumption to focus on the tradeoffs in restoring perennial (in-channel) vs ephemeral (floodplain) habitats to support rearing fish. However, it is worth noting that the inclusion of this process within the modeled scenarios is equivalent to the scenarios that included increased current in-channel and floodplain habitat availability. Thus, the patterns uncovered would not change. Finally, we fully recognize that our evaluations do not consider all the current and potential future conditions that these fish will likely encounter throughout their life cycle (i.e., climate change, contaminants, etc.). Although such extensions could certainly be included in future evaluations, we stress that DSMs are meant to be abstractions of reality to help guide the conversations within the decision-making process. Requisite DSMs that only include the processes relevant to the decision(s) at hand are often preferred in order to avoid unnecessary complexity and, by extension, increase the interpretability of the simulation results and a decision makers ability to understand system dynamics (Phillips, 1984).

Natural resource managers are often faced with difficult decisions on how to best allocate resources to most efficiently and effectively meet restoration goals. Our evaluation suggests that directing resources to restoring perennial in-channel habitats that are reliably available for the duration of the rearing period is optimal when rearing habitats are limiting. This is not to imply that floodplain habitats are unimportant. There is extensive evidence that floodplains serve important roles in lotic ecosystems (Junk et al., 1989; Petsch et al., 2023). Rather, our modeling efforts suggest floodplain habitats do provide additional benefits provided there is sufficient in-channel habitats to support the greater number and larger sized juvenile fish. Importantly, similar to Peterson and Duarte (2020), our results provide quantitative evidence that there are some situations where restoring habitat may have unintended negative impacts on fish populations and the optimal restoration action is no action at all. Thus, our study reinforces that the context of the decision space matters and that no action alternatives are a worthwhile scenario to consider within any decision analytic process.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://github.com/CVPIA-OSC.

Author contributions

JP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. AD: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1428697/full#supplementary-material

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A rapid assessment methodology for quantifying and visualizing functional landscape connectivity

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Context: The number of publications that evaluate or use landscape connectivity has grown dramatically in recent years. But the biological realism of common connectivity assessments remains limited. To address this shortcoming, I introduce a flexible methodology for evaluating functional landscape connectivity that can be quick to implement, biologically nuanced, and straightforward to interpret.

Methods: I combined a US Fish and Wildlife Service land cover map with information from existing empirical studies to develop a movement simulator for the Fender's blue butterfly, an endangered species in Oregon, USA. I use the resulting butterfly model to explore the concepts and mechanics behind my novel connectivity assessment methodology.

Results: My methods are able to identify clusters of connected resource patches, quantify and visualize movement rates between patches, and identify opportunities for enhancing connectivity through restoration and mitigation. My results include an emergent dispersal kernel that captures the influence of movement behavior on connectivity.

Discussion: The methods I introduce are capable of generating detailed yet practical connectivity analyses that can incorporate considerable biological and behavioral realism. My approach is simple to implement, and the requisite data can be modest. The toolkit I developed has the potential to standardize connectivity assessments that use either real or simulated movement data.

KEYWORDS

connectivity, movement, simulation model, circuit theory, graph theory, dispersal kernel

Introduction

Connectivity assessments are assertions about a landscape's ability to facilitate or impede movement (Taylor et al., 2006). In this context, the things doing the moving are typically living organisms, but could also include viral pathogens, inert objects, flows of energy, ideas, and so on. And any measure of connectivity will be context-specific, as the same landscape can be highly connected for one species or quantity, while being poorly connected for others. Connectivity can be a well-defined and objectively interpretable attribute of fractal-dimensioned networks (Schmadel et al., 2018; Sarker et al., 2019; Xingyuan et al., 2023; Clauzel et al., 2024), but tends to be difficult to assess in two or three dimensional landscapes (Guarenghi et al., 2023; Riordan-Short et al., 2023; Iverson et al., 2024). Here, I describe a new methodology for quantifying landscape connectivity in two dimensions.

Relatively few researchers measure landscape connectivity directly, as empirical studies sufficient to do so are difficult to conduct (Fagan and Calabrese, 2006; Ortega et al., 2023; Carroll et al., 2024; Morin et al., 2024), nearly impossible to replicate, and because the likelihood of observing interpatch movements will typically vary with local population sizes and demographic rates (Mcintire et al., 2007). Instead, mathematical models, computer algorithms, and movement simulations are frequently employed to obtain proxies for connectivity. Inferences used to be drawn from fragmentation indices, which are pattern metrics such as shape index, fractal dimension, or contagion (O'Neill et al., 1988; Turner, 1989). Fragmentation indices describe landscape patterns, and have been shown to have a limited ability to anticipate connectivity when the latter is inferred from the outcome of movement simulators (Schumaker, 1996). The methods used to evaluate connectivity have since changed considerably (Mestre and Silva, 2023), due largely to the development of tools that exploit graph and circuit theories (McRae, 2006; McRae and Beier, 2007; McRae et al., 2008; Urban et al., 2009; Perry et al., 2017). These studies, and others, have inferred patterns of animal movements across large landscapes (Carroll et al., 2012; Severns et al., 2013; Hromada et al., 2020; Finerty et al., 2023), identified strengths and weaknesses of protected area networks (Carroll et al., 2012), prioritized conservation and restoration activities (Dickson et al., 2017; Pither et al., 2023), and much more.

Graph theory is the study of mathematical objects called graphs. In this context, graphs are composed of nodes, which may represent quantities like resource patches, and edges, which always represent connections between pairs of nodes. Ecological models building upon graph theory (Urban et al., 2009), which I subsequently refer to as "graph models", require access to a dispersal kernel (Fordham et al., 2014; Proença-Ferreira et al., 2023). Dispersal kernels are mathematical structures describing the likelihood of arrival at all possible future locations, conditioned on an object's present location. Dispersal kernels can take the form of continuous probability density functions, but in graph theory they are typically square matrices. Once a dispersal kernel has been formulated, the mathematics of graph theory can be deployed to reveal a great deal about network or landscape connectivity (e.g., Perry et al., 2017). But the difficulty of collecting empirical movement data (Fagan and Calabrese, 2006) means that dispersal kernels are often derived from cost path estimates or similar measures (Fletcher et al., 2023). Unsurprisingly, conclusions drawn from pattern-based dispersal kernels can suffer from biological oversimplification (Fordham et al., 2014).

Circuitscape and Linkage Mapper (McRae et al., 2008, 2016), which I subsequently refer to as "circuit models", have been adopted widely in ecology, conservation, and other disciplines (Dickson et al., 2019). Circuit models are software applications that use electrical theory to infer landscape connectivity from resistance surfaces (McRae, 2006; McRae and Beier, 2007; Pither et al., 2023). Resistance surfaces are raster maps in which every pixel has been assigned a value indicating how likely (low resistance) or unlikely (high resistance) an object under study would be to enter that cell. Resistance surfaces are often assembled from extensive empirical data sets describing gene flow across complex landscapes (Peterman, 2023; Calderón et al., 2024), or from extrapolations based upon movement information (Finerty et al., 2023). An advantage of resistance surfaces is their generality; these maps need not be species-specific, and the concept is extensible to the study of a wide variety of endpoints of interest (e.g. Tassi et al., 2015; Tarkhnishvili et al., 2016; Dickson et al., 2019; Buchholtz et al., 2023). A limitation stemming from the use of circuit models is that, regardless of the biological nuance embedded within a resistance surface, these tools have no direct way to account for dispersal ability or behavior.

Fragmentation indices measure structural connectivity. Graph and circuit models, in contrast, attempt to capture functional connectivity by shifting the perspective from landscapes to organisms (Carroll et al., 2012; Perry et al., 2017; Dickson et al., 2019; Finerty et al., 2023; Guarenghi et al., 2023; Pither et al., 2023). But the term functional connectivity spans a continuum of biological and behavioral realism that is not thoroughly represented by these models and methods (Drake et al., 2022). For a simple illustration of what is missing, imagine a landscape composed of an array of cells, each having a score indicating its quality. An individual occupying a cell scored one (poor quality) might readily elect to move into a cell scored three (moderate quality). But, for an individual occupying a cell scored five (optimal quality), this option may appear undesirable. Similarly, behaviors that affect movement distance and path tortuosity might be uniquely influenced by an individual's perception of its recent movement history. When incorporated, this type of biological detail is likely to alter estimates of functional landscape connectivity.

Spatial population viability analysis (PVA) models are typically lifecycle simulators linked to landscape maps. Movement-only simulators are lower-complexity models that ignore much of the detail found in a PVA. But in spite of their relative simplicity, movement simulators can still incorporate dispersal ability, account for species-landscape interactions and disturbance, and capture behaviors in which future decisions are influenced by past experience. And simulation modeling has been widely used for evaluating functional landscape connectivity (e.g., Kramer-Schadt et al., 2004, 2011; Revilla et al., 2004; Revilla and Wiegand, 2008; Pe'er et al., 2011; Kanagaraj et al., 2013; Coulon et al., 2015; Diniz et al., 2020). Nevertheless, inferences about connectivity derived from movement models frequently rely upon visual inspections of cumulative dispersal traffic (Allen et al., 2016; Hauenstein et al., 2019; Day et al., 2020; Unnithan Kumar et al., 2022; Hofmann et al., 2023; Urbina et al., 2023), which my results (see below) suggest may be misleading. And we lack generic, reusable methods and tools that transform dispersal information (empirical or simulated) into utilitarian connectivity assessments complementing those obtained from graph or circuit models (but see Hofmann et al., 2023). My study attempts to address both limitations, and to provide readers with a general solution for teasing insights about functional landscape connectivity out of movement data, regardless of its source.

My methods are designed to draw conclusions about functional connectivity from movement data. Species' vital rates and life cycles are not considered, and my results do not forecast population size, structure, extinction risk, or related measures (e.g., Hanski and Ovaskainen, 2000). And while I believe my methods will be useful for prioritizing mitigation and restoration, I have not coupled my workflow to a formal decision-making rubric (e.g., Westphal et al., 2003). I place my work within the context of graph and circuit models, but I do not make direct comparisons between these tools. With regards to circuit models, I instead emphasize the value of obtaining connectivity assessments that are sensitive to species' movement ability and behavior. In the case of graph models, my methods do not constitute an alternative, but rather a means for obtaining biologically nuanced dispersal kernels. I do, however, make an implicit comparison within the context of simulation modeling by exploring the differences between maps of all individual movements versus those made strictly from paths connecting resource patches.

I begin by introducing my connectivity methodology, and then apply it to a simulated population of Fender's blue butterflies (*Icaricia icarioides fenderi*) occupying a small portion of the species' range. My focus is on illustrating the methods I have developed, and the Fender's blue butterfly (FBB) case study is useful in this context (Mcintire et al., 2007). My FBB movement simulator was informed by data obtained from empirical studies (Schultz and Crone, 2001; Schultz et al., 2012; Cheryl Schultz, pers. comm.); and, to the extent possible, its design replicated that of *FendNet*, the original spatially-explicit and individual-based FBB movement simulator (Mcintire et al., 2007; McIntire et al., 2013; Severns et al., 2013).

Materials and methods

Software tools

I wrote a C-language software utility that performs connectivity analysis, which I refer to below as "LINK", since the program identifies resource patches linked by movement. I also developed a suite of complementary algorithms that simplify the processing of LINK input and output. Together, these applications can be assembled into a workflow for conducting rapid, actionable connectivity assessments (Figure 1). While the FBB movement simulations were conducted in HexSim (Schumaker and Brookes, 2018) all of my other analyses were performed using stand-alone utilities. I've made this code available to readers, along with a fully illustrated example connectivity analysis (see Supplementary Material). HexSim is a popular platform for developing spatially-explicit, individual-based life history simulators (Heinrichs et al., 2023; Lyons et al., 2023; Mims et al., 2023; Ransom et al., 2023; White et al., 2023).

The discussion that follows is, in large part, an exploration of the LINK utility and its potential for quantifying and visualizing landscape connectivity. That said, readers with some programming experience should be able to replicate, extend, and improve upon my methods and tools without reliance on HexSim or LINK. And those interested in quantifying connectivity in marine environments, forest canopies, or other spatially-complex systems could adapt my work to 3-dimensional landscapes.

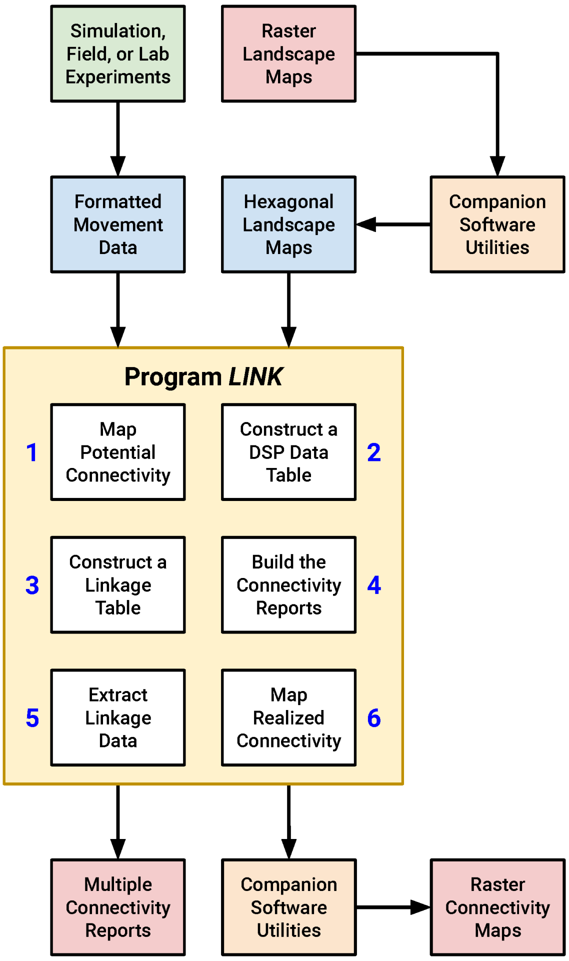

FIGURE 1
A diagram illustrating the proposed connectivity assessment workflow. LINK uses input movement data and landscape maps to generate a suite of connectivity reports and output maps. The process begins and ends with raster imagery, but the LINK program and some of its companion utilities work with hexagonally-tiled landscape maps. LINK itself contains six separate modules that each perform a portion of the overall connectivity analysis.

Study areas

The Fender's blue butterfly case study runs within a map depicting a roughly 14,000 ha area situated in the approximate center of the species' range. This map, which is made up from an array of hexagonal cells, was derived from an ASCII Grid file (https://en.wikipedia.org/wiki/Esri_grid) exported from a geographical information system by staff at the US Fish and Wildlife Service (USFWS). The Fender's blue butterfly study area (Severns et al., 2013) is located in the Cardwell Hills, to the west of Corvallis, Oregon, USA. This site contains one of the largest extant populations of the species.

The USFWS ASCII Grid file representing FBB land cover has an extent of 10,896 columns × 15,231 rows, with each pixel representing a square 0.836 m^2 in size. This makes for a total landscape area of 13,876 ha. I resampled this raster image into a grid of hexagonal cells (a "hexmap") containing 9962 columns and 16,081 rows, slightly in excess of 160M hexagons total. The width (measured between parallel sides) and area of each hexagon are 1.000 m and 0.866 m^2. This fine-resolution map facilitated the simulation of individual FBB movements, which can be as short as three meters (see below). Each FBB land cover hexagon was assigned an integer score equal to the mode of the ASCII Grid pixels falling within that hexagon (Figure 2). Using a mode operator ensured that each hexagon was assigned an integer value, thus preserving the categorical nature of the input ASCII Grid file. Subsequently, 1639 ha that had been assigned a "no data" classification in the ASCII grid file were merged into its "non-habitat" category. Non-habitat is used as a generic designation for developed areas that FBBs will avoid. The resulting map of hexagonal cells contained six land cover categories (Table 1).

Kincaid's lupine (*Lupinus oreganus*) is the sole larval host plant for the Fender's blue butterfly (Liston et al., 1995; Schultz and Dlugosch, 1999; Schultz, 2001). FBB food resources are found within areas classified as lupine or prairie. FBBs can move about within all of the land cover types except for non-habitat, which they will not enter.

There are 140 distinct Kincaid's lupine patches in the FBB map. Of these, 65 are completely isolated by non-habitat, which the simulated butterflies would not enter. (In reality, FBBs will occasionally move across small stretches of non-habitat, such as those attributable to roads. Our FBB habitat map, however, did not include a road network.) That left 75 accessible lupine patches that FBBs might potentially move between. These Kincaid's lupine habitats comprise the focal patches for my butterfly connectivity analysis. The LINK program requires that unique IDs be assigned to every patch in its input patch maps. One of my utilities is designed to perform this labeling task (see Supplementary Material), and I used it to create a Kincaid's lupine patch map suitable for use with LINK.

Movement models

My movement models incorporate behavior, and thus their output stores information about functional landscape connectivity. The LINK utility, which I used to extract this information, imposes

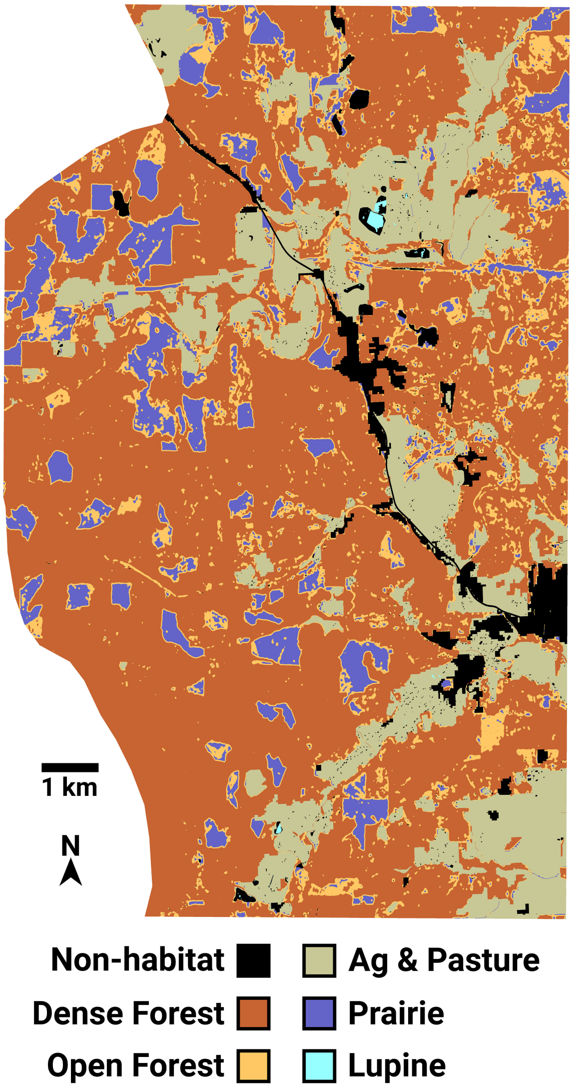

FIGURE 2
The Fender's blue butterfly landscape, represented as a grid of 160 million hexagonal cells. Most lupine patches are too small to be resolved in the image.

TABLE 1 Land cover types and areas from the Fender's blue butterfly hexmap.

Land Cover Type	Hexagons	Hectares
Non-habitat	23,847,287	2066
Dense forest	85,329,621	7390
Open forest	15,565,730	1348
Ag. and pasture	24,738,745	2143
Prairie	10,593,780	918
Kincaid's lupine	123,759	11
TOTAL	160,198,922	13,876

The raster ASCII Grid input file contained the same six land cover classes, plus a separate no-data class. When the hexmap was constructed, the no-data and non-habitat classes were merged.

minimal constraints on model design. Specifically, a suitable model must (a) simulate movement as a sequence of discrete "steps" in which individuals move from a cell to one of its immediate neighbors, and (b) write out all individual movement records in a predefined format (see Supplementary Material). Importantly, the application of LINK need not be limited to modeling studies; my methods can also be used to analyze movement data collected in field or laboratory settings (Finerty et al., 2023).

Grids of hexagonal cells are ideal for simulating movement processes because, unlike square landscape tessellations, all neighbors are equidistant. Hence, HexSim, LINK, and some of the other programs referenced here are designed to work with arrays of hexagonal cells (a hexmap). Nevertheless, landscape data are almost always tiled using arrays of square pixels (a raster). For this reason, I supply readers with software utilities that convert traditional landscape maps into hexmaps, and that convert hexmaps back into raster imagery (see Supplementary Material). This suite of tools provides users with the convenience of beginning and ending with raster maps, while also eliminating artifacts that can accompany the use of such data in movement simulations.

My FBB movement model grew out of a series of conversations with species expert Dr. Cheryl Schultz, who had gathered empirical data describing Fender's blue butterfly turning angles and path lengths as a function of land cover type, and is a co-developer of the *FendNet* model. All simulated FBBs made a series of 250 separate movements, which approximates an actual butterfly's search effort over their single-season lifetime. Each movement step was characterized by a path length (number of steps), autocorrelation (turning angle), and a probability of moving directly towards the species' host plant (Schultz and Crone, 2001), Kincaid's lupine, referred to subsequently as "lupine". In order to match the empirical information, the values used for these parameters were adjusted depending on the land cover class that each butterfly occupied at the time a movement was initiated (Table 2).

In advance of each of the 250 separate movement events, every simulated FBB was placed into one of two behavior classes. Those not already located within lupine evaluated whether they were within 50 meters of a lupine patch. If so, these FBBs used a "go to lupine" probability to determine whether they should move directly towards lupine. FBBs presently within a lupine patch, those nearby who elect not to move directly towards lupine, and butterflies situated far from lupine all moved semi-randomly. Movement path lengths were imposed regardless of behavior class, but autocorrelation only influenced the behavior of butterflies moving semi-randomly. FBBs moving directly towards lupine always took the most efficient path available to them. Butterflies moving semi-randomly blended a correlated random walk with limited emergent taxis towards more "desirable" (Cheryl Schults, pers. comm.) land cover types (Table 2).

TABLE 2 HexSim FBB movement model parameters.

Land Cover Type	Path Length (meters)	Autocorrelation (percent)	Go to Lupine (probability)
Non-habitat	Unused by simulated Fender's blue butterflies		
Dense forest	7	68	0.75
Open forest	7	68	0.75
Ag. and pasture	11	71	0.25
Prairie	11	74	0.25
Kincaid's lupine	3	35	0

The land cover classes have been sorted based on their anticipated desirability for the butterflies.

Both the HexSim FBB model and FendNet were designed using the same empirical data sets and subsequent analysis (Schultz et al., 2012). The most significant differences between the two are that FendNet is a full lifecycle model developed in *SELES* (Fall and Fall, 2001) for which movement behavior is in part expressed via resource-specific turning angles. My model, in contrast, only simulates movement, and it uses autocorrelation rates rather than turning angles. I developed a relationship linking turning angles to autocorrelation rates that facilitated this conversion. The FendNet model was validated using data from a study area 80 km to the south of the Cardwell Hills site (Mcintire et al., 2007). This prior assessment suggests the HexSim simulator is likely to be a reasonable proxy for movement in the Cardwell Hills system.

Because my goal was to evaluate inter-patch connectivity, introducing FBBs into the interior of lupine patches was computationally inefficient. Thus, I initially placed butterflies into every lupine patch edge, excepting those hexagons bordered strictly by lupine and/or non-habitat. Given this criteria, 2797 lupine hexagons qualified as valid starting locations. I ran 1000 model replicates, thus simulating roughly 2.8M butterflies, and generating 0.7B distinct movement records, each varying in length between 3 and 11 hexagons.

Connectivity metrics

The LINK utility ignores movement steps that precede an individual's arrival at its first focal patch. For that reason, I initially placed all simulated individuals into focal patches. LINK begins by aggregating all of the movement records associated with a specific individual into a single continuous movement path. This was somewhat involved for the simulated FBBs, who each moved 250 times in a randomized order, meaning that individual movement records were scattered throughout >200 gigabytes of model output. LINK next measures the rates at which individuals move between focal patches. To do so, it breaks each aggregate movement path into "connecting segments" that begin and end in separate focal patches. Movement steps in the interior of focal patches are not included in connecting segments, but LINK separately records the frequency with which individuals (a) begin and end in the same focal patch, and (b) begin in a focal patch but end in a different land cover type. LINK uses this information when it constructs dispersal kernels that capture the probability of moving between every pair of focal patches.

LINK also constructs a pair of maps that illustrate (a) "potential connectivity", defined as the cumulative number of times each hexagon was visited, and (b) "realized connectivity", which only records visitations associated with connecting segments. Potential connectivity may be thought of as an inverted emergent resistance surface (high potential equaling low resistance) that conflates absence and avoidance. In contrast, realized connectivity serves as a visual representation of a dispersal kernel. Finally, LINK uses the connecting segments to construct a report describing "connectivity clusters", defined as collections of focal patches linked by movement. This report includes values for "cluster traffic", the number of focal patches per cluster, and the IDs of every patch making up each cluster. A cluster's traffic is defined as the number of connecting segments linking all of the focal patches it contains.

While developed independently, the initial stages of my connectivity analysis are reminiscent of a portion of the methodology published by Hofmann et al. (2023). That being the case, our approaches for drawing conclusions about functional landscape connectivity are distinct yet complementary. Hofmann et al. (2023) and others (e.g. Carroll et al., 2012; Sarker et al., 2019), use a graph theory metric termed "betweenness centrality" to infer connectivity from collections of simulated movement paths. In contrast, my strategy involves isolating the portions of movement paths that link resource patches, and using this information to identify and interrogate connectivity clusters.

Results

LINK's analysis of the FBB movement data revealed the presence of nine separate connectivity clusters (Figure 3), which ranged in size from 3 to 13 lupine patches. Cluster area and traffic varied across three and four orders of magnitude, respectively (Table 3). Of the 75 accessible lupine patches, 59 were included in the nine connectivity clusters. The remaining 16 accessible patches were functionally disconnected.

I used LINK's maps of potential and realized connectivity to more closely examine clusters 1-3, 7-8, and 9 (Figure 3). Based on potential connectivity, almost all of the lupine patches in the vicinity of clusters 1-3 would appear to be part of a single expansive "supercluster". In contrast, the map of realized connectivity (Figure 4), and LINK's cluster analysis, suggest that functional connectivity is limited in this region. A direct comparison of the two connectivity maps (Figure 4) indicates there is a possibility of reconnecting clusters 2 and 3, presumably via habitat restoration, as a large number of simulated butterflies explored the intervening landscape. In contrast, many fewer butterflies moved within the gap separating clusters 1 and 2. These results also suggest that cluster 2 might be extended to the east. Finally, the realized connectivity data suggests that cluster 3 itself is only tenuously connected, and likely vulnerable to future habitat loss.

Similarly, while the map of realized connectivity suggests that clusters 7 and 8 are functionally distinct, the map of potential connectivity indicates that the possibility exists to tie this entire area into a single connected supercluster (Figure 5). Given that clusters 7 and 8 exhibited the system's largest cluster traffic (Table 3), the relative benefit of targeting this area for restoration may be high. A parallel inspection of cluster 9 (Figure 6) suggests that restoration activities in the immediate vicinity of the existing functionally connected lupine patches might benefit the FBB population; but the creation of a robust new supercluster here may require substantial investment.

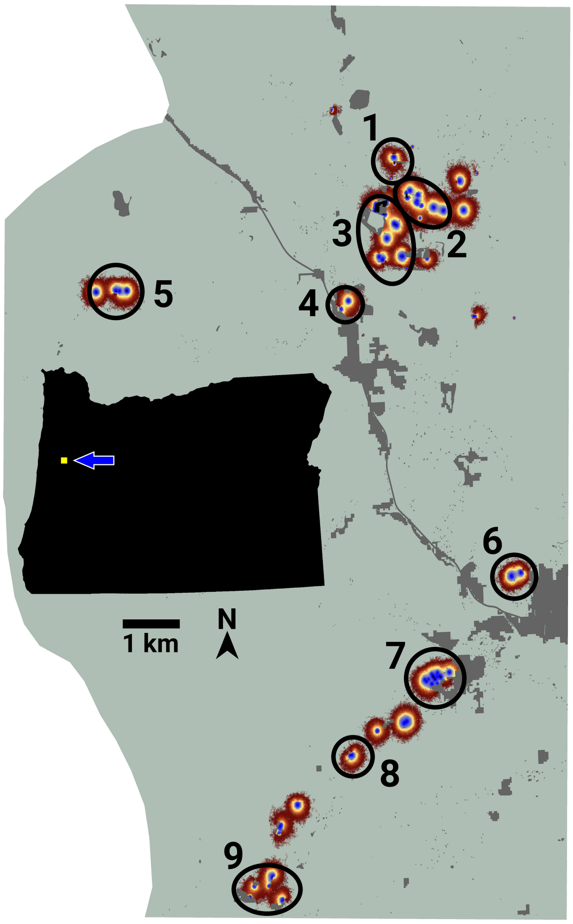

FIGURE 3
An image of potential connectivity for the Fender's blue butterfly system. Numbered ovals indicate the approximate locations of nine emergent connectivity clusters. The inset map shows the study area's location relative to the state of Oregon, USA.

LINK generated an emergent FBB dispersal kernel in the form of a sparse square matrix with dimension 140 (the number of lupine patches) containing 19,600 cells. This matrix, which is best imaged as a heat map due to its size (Figure 7), has values that range between zero and 0.996. The value of the cell in column i and row k represents the probability that a FBB located in lupine patch i would subsequently move to patch k. The sum of column i equals the probability that a butterfly located in patch i would move to any lupine patch (including itself), while 1.0 minus this quantity is the likelihood that a FBB leaving that location would stop moving somewhere in the non-lupine matrix. The sum of row k represents the probability that a butterfly would travel to patch k from any other lupine patch, including itself.

TABLE 3 The LINK connectivity cluster analysis for the FBB model.

	Cluster Traffic	Lupine Patches	Cluster Area
Cluster 1	349	3	929
Cluster 2	346,486	13	2591
Cluster 3	496,290	10	25,818
Cluster 4	248,465	3	45
Cluster 5	368,602	5	943
Cluster 6	331,611	3	168
Cluster 7	1,025,837	13	2909
Cluster 8	540,085	3	50
Cluster 9	66,593	6	947

Lists of individual patch IDs have been replaced with cluster area, measured as the total number of lupine patch hexagons. LINK assigns cluster IDs in map order, from the upper-left to lower-right.

Discussion

Researchers commonly use graph theory, circuit models, and spatial simulators to quantify landscape connectivity. Models incorporating graph theory (e.g. Bastian et al., 2009; Foltête et al., 2012) use putative dispersal kernels to assess the importance of network "nodes" and "edges". But by necessity, dispersal kernels are often derived from landscape geometry rather than movement data (Dickson et al., 2019; Finerty et al., 2023); in such cases, conclusions drawn from these models can lack realism (Fordham et al., 2014). And even when sufficient movement data are available, it can prove difficult to extract a dispersal kernel from this information. The Circuitscape family of tools (McRae et al., 2008, 2016) infer patterns of landscape connectivity from simulations of electrical current flowing across resistance surfaces. But current flow cannot capture movement behavior, and will only fall to zero where resistance is infinite. In contrast, movement simulators can replicate complex individual behaviors, and their estimates of movement rates may drop to zero in any location due to energetic constraints, perceived threats, and so on. Unfortunately, generic, flexible tools that can convert movement data (simulated or real) into connectivity assessments have not been available, forcing researchers to develop independent solutions on an as-needed basis.

Here, I have introduced a general methodology for extracting dispersal kernels from movement data. LINK's emergent dispersal kernels, which retain the biological detail captured within real or simulated movement data, can be substituted into existing graph models, thus increasing their realism. My software can also generate assessments of functional landscape connectivity directly from any properly-formatted movement dataset. LINK's illustrations of potential connectivity are reminiscent of the current flows obtained from circuit models, and of the maps of cumulative individual movement paths derived from simulation modeling experiments. But the considerable differences between LINK's potential and realized connectivity maps highlight the utility of discriminating between all landscape locations that have been visited collectively, versus just the sites that were traversed during successful movements between resource patches. Policy recommendations informed by the former are likely to differ significantly from those influenced by the latter.

I used the Fender's blue butterfly case study to explore the differences between potential and realized connectivity, and to illustrate how maps of these quantities might be useful for ranking management strategies. Simulated FBBs frequently proved unable to move between lupine patches that exhibited high potential connectivity. For example, maps of potential connectivity suggest the lupine patches in the vicinity of connectivity clusters 1, 2, and 3 might be a low priority for habitat restoration (Figure 4). The results from my evaluation of realized connectivity indicate exactly the opposite. Similar mismatches arose in the neighborhood of connectivity clusters 7

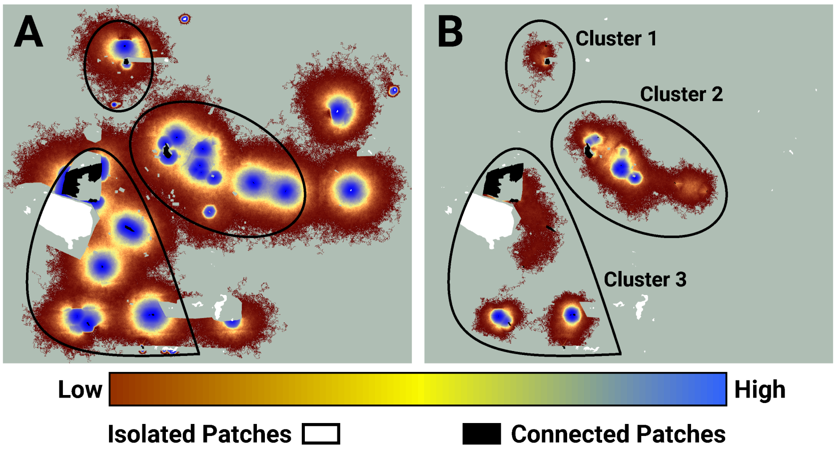

FIGURE 4
An image of potential connectivity in the vicinity of clusters 1, 2, and 3 **(A)**. The image of realized connectivity used to identify the three clusters **(B)**. The relative values of both potential and realized connectivity are indicated by the colorbar. Non-habitat and areas unused by FBBs are shown in light green. The black outlines indicate the approximate cluster locations. Isolated (white) and connected (black) lupine patches have been superimposed on the images. Some lupine patches may be too small to resolve. Each panel is 2.2 km in width.

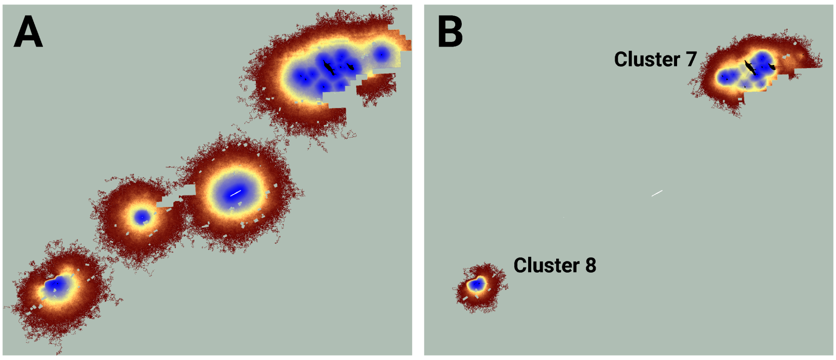

FIGURE 5
An image of potential connectivity in the vicinity of clusters 7 and 8 **(A)**. The image of realized connectivity used to identify the two clusters **(B)**. Isolated (white) and connected (black) lupine patches have been superimposed on the images. Some lupine patches may be too small to resolve. Each panel is 2.2 km in width. See Figure 4 for additional color-related details.

and 8 (Figure 5) and cluster 9 (Figure 6); they are likely ubiquitous across the FBB system.

Data is not currently available to directly test the validity of LINK's FBB connectivity assessments. The most similar existing connectivity analysis is substantially different, and was conducted in a separate portion of the species' range (Mcintire et al., 2007). While a great deal of information has been gathered on FBB movement in various portions of the species' range (e.g., Schultz et al., 2012), the only other Cardwell Hills connectivity study (Severns et al., 2013) produced findings that, by design, cannot be compared to LINK's output. The results from the present study should therefore be approached as hypotheses to be challenged and refined. More generally, the methodology I've described here will benefit from future applications involving other ecological systems, landscapes, and life histories.

Conclusions

Graph- and circuit-based connectivity assessments are compelling and influential, but they frequently incorporate little biological nuance (Drake et al., 2022). In contrast, spatial PVAs have been trending towards realism and defensibility (D'Elia et al., 2022; Pili et al., 2022; Heinrichs et al., 2023), though this has been accompanied by increasing development time and effort (e.g. Snyder et al., 2019). Movement-only simulators provide a compromise; they can capture sophisticated individual behaviors (Schultz and Crone, 2001; Brown et al., 2017), species-landscape interactions, and disturbance, while still being parsimonious and quick to assemble. And the data generated by these models are uniquely well-suited for catalyzing new insights into functional landscape connectivity. But researchers lack generic methods for

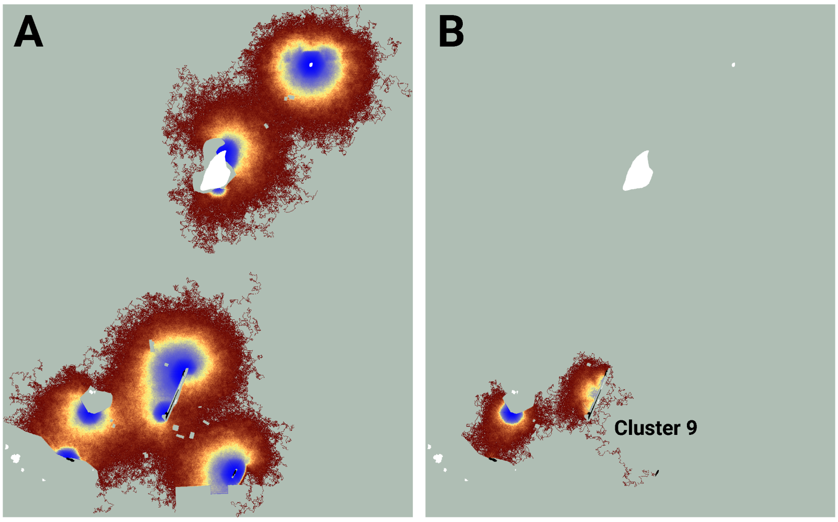

FIGURE 6
An image of potential connectivity in the vicinity of cluster 9 **(A)**. The image of realized connectivity used to identify the cluster **(B)**. Isolated (white) and connected (black) lupine patches have been superimposed on the images. Some lupine patches may be too small to resolve. Each panel is 1.4 km in width. See Figure 4 for additional color-related details.

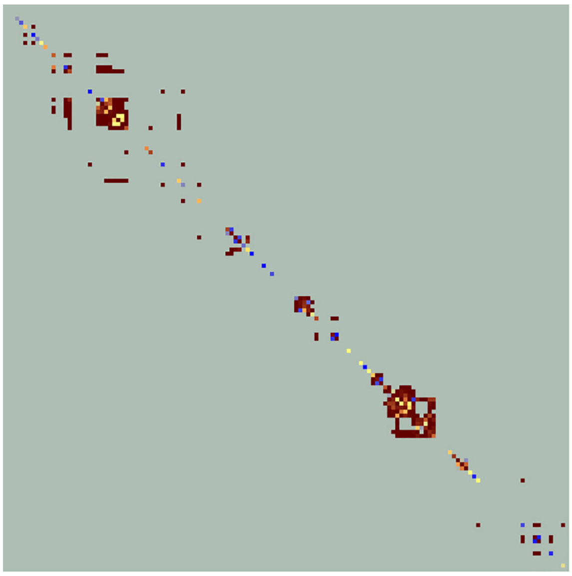

FIGURE 7
A heat map analog of the emergent FBB dispersal kernel, which is 140 × 140 lupine patches in size. Zero-valued cells are displayed in light green. Cells falling along the diagonal indicate movement rates from a patch to itself. Asymmetries imply unequal directional rates of exchange between pairs of lupine patches. Connectivity cluster size is correlated with the number of off-diagonal cells lying within specific portions of the image. See Figure 4 for additional color-related details.

inferring functional connectivity from simulation model output, and thus frequently end up developing study-specific software and algorithms that are not readily transferable to others. Here, I provide a general solution constructed with reuse in mind.

My LINK utility is designed to extract connectivity metrics from movement data regardless of how this information was obtained. The analyses I've described involve five steps: (1) designing a movement model and running simulations, (2) processing the simulation output, (3) generating a dispersal kernel, (4) mapping and visually inspecting both potential and realized connectivity, and (5) performing a connectivity cluster analysis. LINK automates steps 2-5, thus greatly simplifying the workflow. Though I used HexSim for simulating FBB movement, all my other pre- and post-processing steps were performed by stand-alone software utilities. To facilitate the transfer of this technology, I have provided a worked example of the entire process, beginning with a land cover map and ending with a full connectivity analysis (see Supplementary Material). This illustration does not require the use of HexSim, thus minimizing the investment required to replicate and improve upon my methods.

By isolating Fender's blue butterfly movements that join distinct lupine patches, I was able to identify connectivity clusters, and quantify rates of movement between cluster patches. My visual comparisons of potential versus realized connectivity suggest where restoration efforts might most effectively enhance landscape connectivity, and can help identify resources at risk of becoming functionally disconnected. Additionally, LINK's emergent dispersal kernels should facilitate the application of graph-theoretic models to conservation challenges set within complex landscapes. Once a dispersal kernel has been obtained, the remaining components of a graph model are relatively straightforward to assemble. LINK's results also have the potential to simplify future PVA model development. For example, smaller more computationally efficient predictive models could be developed separately for each of LINK's emergent connectivity clusters. And these new focal-area PVAs would no longer need to simulate movement, as they could instead use a pre-computed dispersal kernel.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

NS: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1412888/full#supplementary-material

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Consolidating diverse modeling methods and spatial prioritization for multispecies connectivity planning

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Introduction: Given the different life histories and movement behaviors of diverse species, reconciling conservation measures to benefit all species is a critical concern for landscape conservation planning. Understanding land cover composition and finding multispecies movement routes across heterogeneous landscapes are crucial to maintaining many target species. The primary objectives of this study were to determine the optimal environment in Florida that promotes multispecies connectivity in landscapes increasingly threatened by rapid suburban development and to enhance methods for delineating the state's ecological networks.

Methods: Potential functional connectivity of the focal species with statewide distributions and are considered priorities because of the historical and current threats to their population viability, such as the Florida black bear (*Ursus americanus floridanus*), Florida panther (*Puma concolor coryi*), eastern indigo snake (*Drymarchon couperi*), and southern fox squirrel (*Sciurus niger niger*), were modeled using Linkage Mapper, Omniscape, and resistant kernels. We combined quantiles from each method for a single species combination approach to leverage the results from the three models for planning purposes. Subsequently, we integrated the results into a novel multiple species, multi-model connectivity mapping approach. Following the corridor analysis, a comparison was made between multispecies connectivity maps, current managed conservation lands, and the main priority areas for the Florida Wildlife Corridor, a previously developed planning network of natural hubs and corridors. Finally, we used the spatial prioritization software Zonation to identify areas of conservation priority, while also illustrating the impacts of infrastructure (built infrastructure, roadways, mining, and future development 2040 and 2070 projections) and threats from human activity (landscape fragmentation, recreation, pollution, contamination, and clean-up sites).

Results: The study identified priority areas for all four species, with a particular focus on areas not currently protected. The connectivity models showed significant overlap with current managed conservation lands and the main priority areas for the Florida Wildlife Corridor. Pinchpoint areas or bottlenecks were identified as needing fine-scale incorporation into spatial planning. Using the spatial prioritization software Zonation, we identified areas of conservation priority and illustrated the impacts of infrastructure and threats.

Discussion: The results indicate that species-relevant connectivity models incorporating a group of focal species with both complementary and opposing habitat requirements can better inform biodiversity conservation and landscape design decisions. This multi-model approach provides a robust framework for identifying and prioritizing areas for conservation, particularly in landscapes facing rapid suburban development. Integrating multispecies connectivity models into conservation planning can enhance the effectiveness of ecological networks and contribute to the long-term viability of diverse species in Florida.

KEYWORDS

multispecies connectivity, spatial conservation prioritization, corridor design, infrastructure, landscape conservation planning, landscape architecture

Introduction

In the context of rapid environmental change, the presence and condition of habitat in remaining conservation areas, their connectivity, and their ability to withstand disturbances and human impacts are all critical for preserving biodiversity and facilitating movement of multiple species (Haddad et al., 2015). In a mosaic of human-altered landscapes, complex impediments to species' movement make protecting biological patterns (habitats, land cover) and processes (movement, gene flow) across large landscapes a priority for conservation action (Donald and Evans, 2006; Baldwin et al., 2012; Cushman and Landguth, 2012; Anderson et al., 2015; Cox et al., 2017; Carlier and Moran, 2019; Correa Ayram et al., 2019). Simulations of landscape connectivity for multiple species in large mixed-use landscapes, where fragmentation threatens movements and gene flow, have shown the need to establish protected corridors between suitable habitat sections as anthropogenic activities degrade and develop land in rapidly urbanizing areas (Brodie et al., 2015; Bauder et al., 2021; DeMatteo et al., 2023).

Due to differences in habitat suitability, dispersal distances and home range, and sensitivity to human activities, conservation plans to enhance connectivity for one species may not be effective for another (Brodie et al., 2015; Wang et al., 2018). Large, wide-ranging animals (commonly referred to as "flagships" or "umbrella species") (Breckheimer et al., 2014; Wang et al., 2018; Shi et al., 2019; Shen et al., 2020) with large area requirements are extensively studied in connectivity research because it is believed that they provide a connectivity umbrella for other species. However, one wide-ranging animal may not provide a connectivity umbrella for other large-ranging species (Cushman and Landguth, 2012), and furthermore, habitat generalists may not serve as an umbrella for habitat specialists (Beier et al., 2011, 2008). If the principal objective were to maintain ideal corridors for all species, neglecting to consider these cross-taxon variations may undermine the efficacy of corridors and incur additional financial expenses (Dilkina et al., 2017).

To better understand the distribution and habitat connectivity of numerous species, researchers and conservation planners are examining connectivity, corridors, bottleneck and impedance zones that allow or hinder movement between diverse habitats using several spatial tools based on circuit theory including Omniscape (Tessier et al., 2020; Landau et al., 2021), Linkage Mapper (McRae and Kavanagh, 2011), and resistant kernels (Compton et al., 2007; Zeller et al., 2018). Connectivity model results can vary for different modeling methods, with outputs for designing corridors varying due to the underlying methodologies. In order to maintain population stability and mobility in dynamic rapidly urbanizing environments, it is possible to map multi-species connectivity by overlapping mapping results from a single model such as least-cost pathways or maximum current flow (Marrotte et al., 2017; Sahraoui et al., 2017; Liu et al., 2018; Ashrafzadeh et al., 2020; Lines et al., 2021; Riggio et al., 2022; Spontak and Hoctor, 2017; Santini et al., 2016). Few attempts have been made to incorporate multiple models into a single, comprehensive framework that can leverage the strengths of different methods (Gallo et al., 2020; Jennings et al., 2020a, 2020b).

Besides modeling habitat suitability and connectivity, environmental stressors should be considered when prioritizing areas for conservation planning (Moilanen and Arponen, 2011).

Existing connectivity corridor design methods often fail to prioritize spatial conservation and often fail to consider non-ecological data, such as crucial infrastructure or threat elements that influence land-based acquisitions (state/federal/local government and private conservation actors) to procure lands for corridor conservation, such as nearby pollution features or other human pressures. The creation of operational models and decision support tools, or simplified conceptualizations of processes for implementing conservation action in priority conservation areas, is indispensable for directing conservation planning efforts when allocating limited conservation funds (Knight et al., 2006; Knight et al., 2009; Vizek and Nielsen-Pincus, 2017; Offer, 2020; Sparks, 2021).

Functional landscapes are a global issue, and are especially important in Florida, a rapidly developing state within a region designated as a biodiversity hotspot (Noss et al., 2015). Due to rapid urban development and increasing human population, the natural habitat of many species has been compromised (Zhu M. et al., 2015; Zhu M.-J. et al., 2015; Rodgers and Pienaar, 2018; Bauder et al., 2021; Davis et al., 2021). Florida has experienced considerable landscape transformation due to urbanization and changes in land use, the latter of which is primarily attributable to the rapid immigration of new residents (Kautz et al., 2007; Reece et al., 2013; Carr and Zwick, 2016; Volk et al., 2017). Previous land use/land cover change research has shown that Florida's natural and semi-natural vegetation base declined between 73,063 and 93,938 ha annually between 1985–1989 and 2003, suggesting a true intensification of the central portion of the Florida peninsula (Kautz et al., 2007). The Florida Ecological Greenways Network (FEGN) and Florida Wildlife Corridor (FLWC) (The FEGN is the modeling process and corridor planning tool that serves as the foundation for the legally defined FLWC) use ecological geodesign and spatial prioritization to create a network of natural areas, working lands, and habitat corridors for priority species to protect and preserve the state's biodiversity. The FEGN modeling process includes Florida panther and Florida black bear priority areas and connectivity, other fragmentation sensitive or landscape dependent species habitat models, habitat for additional rare or focal species, landscape matrix and underrepresented natural communities, priority wetlands and floodplains, priority natural areas, the existing habitat network, biodiversity, critical lands and waters, and multiple landscape connectivity models (major river, coastal-to-inland, xeric) (Hoctor and Volk, 2021a).

The establishment of an extensive network of conservation lands can be attributed to conservation programs administered at federal, state, and local levels that now encompasses 31% of the state's total area (Boughton et al., 2019). In 2021, the FLWC corridor design was officially recognized by Florida state law, and beginning in 2024, there would be recurrent financing for the purchase of conserved property (Brodeur, 2021; Hutson, 2024). In reports detailing the FLWC's strategic prioritization for incorporation with the Department of Environmental Protection's Division of State Lands (DSL), Hoctor and Volk (2021a) show that corridor design is constantly evolving through iterative processes, including the latest methodological data layers and science, as informed by a network of statewide governance and environmental management stakeholders.

Improving decision support tool science and techniques is crucial for communicating with land protection staff, other conservation agencies and NGOs, and other governmental officials. We wanted to investigate new approaches and tactics for boosting priority species integration into the wildlife corridor beyond the current FLWC's wildlife and environmental connectivity layers and show methods for further incorporating threats and infrastructure into the modeling framework. The species chosen for these analyses were selected through a collaborative stakeholder process based on available data on distribution, occupied patches, and previously developed habitat suitability models, as well as priority for conservation due to perceived losses in population in the past decade and urgency for conservation and recovery. Statewide significance constituted one of the factors associated with inclusion in the study, whereas species with limited ranges are better analyzed at a county or subregional scale. Four representative vulnerable species with different landscape mobility, yet with a statewide distribution, were chosen: Florida black bear (*Ursus americanus floridanus*), Florida panther (*Puma concolor coryi*), eastern indigo snake (*Drymarchon couperi*) and southern fox squirrel (*Sciurus niger niger*) (see Supplemental Information 1 for background on these species including home ranges and any information on dispersal). Our goals were to: a) assess and compare connectivity patterns among species, b) merge different connectivity modeling results to identify areas of commonality between modeling approaches for each species, and c) examine integrated connectivity models of the four species combined. These approaches merge a multi-model connectivity procedure into map results for different species to integrate new methodologies for assessing strategic connectivity priorities across the state.

After conducting the corridor analysis, multispecies connectivity maps were compared to the currently managed conservation lands and the principal priority areas of the FLWC to illustrate any areas of overlapping connectivity. Finally, we further illustrated potential threats and infrastructure development using the spatial prioritization software Zonation, while also illustrating the effects of overall landscape integrity, human activities (recreation, pollution, contamination, pesticides, and clean-up sites) and infrastructure (built infrastructure, roadways, mining, and future development projections for 2040 and 2070) on ecological connectivity planning. While various iterations of the FLWC do remove infrastructure and development effects from the strategic prioritization, this study investigates potential ways to include rankings of infrastructure and future development threats into visualizations and potential for higher prioritization status and higher precision for strategic areas within multispecies corridor designs.

Methods

Study area and core habitat areas

The state of Florida comprises an extensive land area of 151,900 km^2, which showcases a diverse array of 81 natural communities

(Florida Natural Areas Inventory, 2010). Florida exhibits humid and subhumid subtropical and tropical climates as its primary climatic conditions. The state's topography primarily consists of low terrain, with elevations not surpassing 100 meters (Boughton et al., 2019). Formally designated a biodiversity hotspot, the area is situated within the broader North American Coastal Plain, which extends throughout the southeastern region of the continent (Noss et al., 2015). There are 3038 vascular plants and 4,368 species of fauna in Florida, in addition to 269 endemic animal species (NatureServe, 2021). There are numerous species protected under state (44) and/or federal (89) law in Florida (Boughton et al., 2019). Many of Florida's diverse range of species and habitats are threatened by climate change, sea level rise and land cover change (Hoctor et al., 2000; Reece et al., 2013; Romañach et al., 2020). This area is well-suited for testing corridors that support numerous species because of the patchwork of protected areas and the present plans for the Florida Wildlife Corridor with many vulnerable species still occupying the private land outside of the protected areas (Hoctor et al., 2007; Hoctor and Volk, 2021b, 2000).

Our study focused on large landscape connectivity across a large land mosaic comprised of conservation, agriculture, mining, rural, urban and suburban land uses. Natural vegetation has been fragmented and altered from urbanization (Lopez et al., 2004; Harveson et al., 2007; Carr and Zwick, 2016; Davis et al., 2021), large-scale agricultural uses like citrus and plantation forestry (Repenning and Labisky, 1985; Means et al., 1996; Fox et al., 2007; Andreu et al., 2008), cattle grazing (Sonnier et al., 2023), phosphate mining (Caple, 2017; Duan et al., 2021; Khare et al., 2021), as well as oil and gas operations (Baynard et al., 2014). Numerous factors negatively affect the health of the bioregion and its species, including long-term suppression of fire (Varner et al., 2005; Lindemann, 2009), deforestation (Enge and Marion, 1986), pesticides (Facemire et al., 1995; Marburger et al., 2002; Tavalieri et al., 2020; De María et al., 2021), air pollution (Edwards et al., 2019), invasions of non-native flora and fauna (Engeman et al., 2019; Assis et al., 2020; Conyers and Roy, 2021; Hardin, 2007; Julian et al., 2012; Hiatt et al., 2019; Sinclair et al., 2020), groundwater contamination (Outman, 2020; Heil and Muni-Morgan, 2021; Li et al., 2022; Vermeylen et al., 2022; Lapointe et al., 2023), sea level rise (Reece and Noss, 2014; Zhu M. et al., 2015; Zhu M.-J. et al., 2015; Davis et al., 2021), and fluctuating climatic conditions (Catano et al., 2015; Montero et al., 2018; Abernathy et al., 2019; Zampieri et al., 2020).

TABLE 1 Displays the simulated dispersal distance, reported home range from literature, and study reference for the focal species.

Species	Simulation	Literature Home Range	Study
Florida Panther	321 km (200 miles)	217.04 km^2 (48.38–765.35 km^2) female	U.S. Fish and Wildlife Service, 2020b
Florida Black Bear	200 km (125 miles)	31.16 ± 8.23 km^2 female and 220.93 ± 28.48 km^2 male	Karelus et al., 2016
Eastern Indigo Snake	10 km (6.2 miles)	5-8 km^2	Hyslop, 2007
		1.13 km^2 (113 ha) female, 2.33 km^2 (233 ha) males	Metcalf, 2017
		33-354 ha (0.33-3.54 km^2) female (MCP), 140 - 1,528 ha (1.40-15.28 km^2) male (MCP)	Hyslop et al., 2014
Southern Fox Squirrel	3 km (1.86 miles)	0.34 km^2 (36.7 ± 1.3 ha)	Prince and DePerno, 2014

Priority areas for focal species

Previously developed core habitat and species occurrences were used for each of the four species as our core priority areas (Supplementary Information 2 - Figure S1). Our goal was to simulate connectivity between core conservation areas that could support potential breeding populations using simulated movement thresholds previously identified in the literature (Table 1).

To create core habitat patches for Florida Panther, we identified core conservation areas that overlapped with the most suitable areas corresponding to previously developed habitat suitability models (Frakes et al., 2015; Frakes and Knight, 2021). The patches were rasterized using ESRI's ArcGIS pro-3.3. The Florida Natural Areas Inventory (FNAI) Florida Managed and Conserved Lands (FMLA) layer was rasterized to remove any boundary layers and reduce it to continuous patches. The new FLMA contiguous polygons were clipped to the habitat patches and subset to any patch larger than 228 km^2, which was decided based on known home range of females (Table 1). Due to the lack of realistic long-term connectivity and the foreseeable threat of development, two patches—the Withlacoochee State Forest and Goethe State Forest patches—were deleted. In addition, we incorporated expansive contiguous regions that are presently occupied by the Florida panther (Big Cypress, CREW, and OK Slough) but are not currently protected areas.

To create core patches for Florida Black Bear we subset the Florida Fish and Wildlife Conservation Commission's (FWCC) defined occupied areas from the 2018 Florida black bear range map. We used a minimum area threshold of 202 km^2 to subset the analysis to core breeding areas. We aimed to simulate connectivity (200 km) between larger breeding areas to identify the most vital pathways that maintain connectivity between sub-populations.

For indigo snakes, the core populations were provided by FNAI based on a collaboration with the USFWS species status assessment (U.S. Fish and Wildlife Service, 2018; Bauder, 2019).

The southern fox squirrel occurrences were provided by FWCC. The dataset includes all relevant confirmed locations for the fox squirrel, although may not adequately represent the full range of their habitat. We did not alter these layers prior to use in the modeling efforts.

Resistance surfaces

For Florida panthers, we used the previously developed random forest model (Frakes and Knight, 2021). For Florida black bear, an averaged, ensemble modeling strategy was used (Poor et al., 2020). They applied maximum entropy and Mahalanobis distance to model black bear habitat suitability in Florida. The eastern indigo snake (U.S. Fish and Wildlife Service, 2018; Bauder, 2019) and southern fox squirrel (FWC, 2017) habitat suitability models were both previously developed using MaxEnt.

When designing corridors for long-distance dispersal by mobile animals, previous research on resistance surfaces has suggested employing a negative exponential function to convert habitat suitability into resistance (Trainor et al., 2013; Mateo-Sánchez et al., 2015; Keeley et al., 2016). This has been presented as an alternative to the linear inverse of habitat suitability. We thought that the linear inverse of habitat suitability would be suitable for the fox squirrel whose range was simulated upwards of 3 km for dispersal, and therefore not long distance. For species with wider range and more general dispersal we chose negative exponential scaling. For Florida panther and Florida black bear we used a scaling value of -8, and for eastern indigo snake a scaled value of -2. The selection of these values was determined based on the most rational estimation of long-distance dispersal for the given species. Long-distance dispersal or pre-dispersal scouting may require animals to traverse moderately suitable settings, where resistance increases only modestly as suitability decreases from its maximum value but increases dramatically at lower suitability values. The exponential scaling was simulated with values between -2 and -8 to determine the realistic scenarios, using the following equation, where h represents the raster values and R represents the scaling value.

$$c = 100 - 99 \ \ x \ \ \left(\frac{1 - \exp\left(-Rx \ \ h\right)}{1 - \exp\left(-R\right)}\right)$$

Prior to running the connectivity models the values were transformed linearly between 1–100.

$$f(h) = (h - \min)/(max - \min)$$

Values closer to one hundred indicate the most resistant conditions, whereas values closer to one indicate the most suitable or least resistant conditions.

Least cost corridors

Linkage Mapper 3.1 was used to map least cost corridors using tools in the ESRI ArcGIS Desktop 10.8.2 toolbox (McRae and Kavanagh, 2011). The following parameters were applied based on literature-based home range or dispersal information (Table 1). Florida panther, a Euclidean distance of 321km to reflect dispersal, and a corridor truncation of 321km; Florida black bear, a Euclidean distance of 200km to reflect the potential dispersal on the landscape, and a corridor truncation of 200km; eastern indigo snake, we used core populations with a bounding circle and a 5m buffer, a Euclidean distance of 20km, and truncated corridors to 20km; southern fox squirrel, we used occurrences, a Euclidean distance of 3km, and a truncation of corridors to 8km. The Linkage Mapper outputs were reclassified using 1-10 quantiles to represent percentages.

Omniscape

Omniscape was implemented in Julia 1.8.5 (McRae et al., 2016; Landau et al., 2021). Within Omniscape we used a moving window radius of 100 pixels, and a block size of 21 pixels due to the statewide scale of our study, and yet need to capture finer scale features. For our analyses we used the following results from Omniscape: 1) cumulative current flow, which is a sum of the current maps from all iterations of the moving window analysis and 2) normalized flow which is derived by dividing the current flow by the potential flow, and gives out puts for impeded (< -0.5 SD from mean), diffuse (-0.5 to 1 SD from mean), channelized (1 to 2 SD from mean) and intensified flow (>2.0 SD from mean) (TNC, 2023). The cumulative current flow outputs were reclassified using 1-10 quantiles.

Resistant kernels

The resistance surface was modeled in UNICOR v2.0 (UNIversal CORridor and network simulation model) in conjunction with the least-cost resistant kernel parameterization (Landguth et al., 2012). Using Spatially Balanced Points, point arrays were constructed across the landscape for Florida panther (n=500), Florida black bear (n=3000), indigo snake (n=500), and fox squirrel (n=1000). The resistant kernel outputs were reclassified using 1-10 quantiles.

Comparing models

We computed correlations between the combined models to compare the effectiveness of individual species in predicting landscape connectivity and habitat use for the other species in this study. We used Band Collection Statistics in ESRI ArcGIS pro 3.3 to compute the correlation between layers, using the output values of the correlation coefficients, which represent the relationship between two datasets.

Overlapping priorities

Using the final integrated combined connectivity model for the four priority species, we evaluated the ability of the current protected area portfolio to preserve connectivity for these species as well as the Florida Wildlife Corridor's ability to meet the specific needs of these species. To conduct a fine-scale case analysis, a specific subset that had been identified as a conservation void outside of the corridor plans but had high levels of prospective multi-species corridor connectivity was emphasized.

Assessing pinchpoints

A multi species corridor subset was in southern Alachua County and was evaluated for conservation. Our research used two ways to determine population bottlenecks or limited flow in the landscape or corridor. LinkageMapper uses Circuitscape to find pinch spots in the corridor. Similar to Omniscape, normalized current flow statistics may be partitioned to detect impeded, intensified, and channelized flow and visualize geographical conservation priorities. Our goal was to leverage both results for a visualization of each species-specific impeded and channelized flow according to the different outputs. To accomplish this objective, we reclassified the outcomes as quantiles. For LinkageMapper Pinch points the upper 20–50 percent was assigned a value of 1, and the upper 10–20 percent was assigned a value of 2. The Omniscape results were reclassified as follows: intensified as a 1 and channelized as a 2. Subsequently, the Linkage Mapper Pinchpoints and Omniscape intensified and channelized flow were combined using a scale of 1-4 to emphasize regions of overlap between the two outcomes. In our results, we also incorporated the Omniscape impeded category to emphasize regions that had already been impeded for each specie based on the underlying resistance surface.

Spatial conservation prioritization

In order to identify the priority areas for the conservation of corridor connectivity in Florida, we used Zonation v5 spatial conservation prioritization software (Moilanen et al., 2005; Moilanen, 2007; Lehtomäki et al., 2016). We compiled numerous geospatial data related to infrastructure (development, mines, transportation, utilities, recreation) and threats to environmental quality (pollution sites, cleanup sites and water pollution) as well as a landscape integrity layer from the Critical Lands and Waters Identification Project (Oetting et al., 2016). We had a panel of seven experts (3 University of Florida, 1 University of Maryland, 1 USFWS, 1 FWCC, and 1 private consultant) rank the infrastructure against the connectivity map for severity of threat to the corridor (see S3 for detailed information about data layers). Experts were advised to rank the infrastructure against the connectivity layer, which was weighted with a 1, on a scale of 0-2.

The output of Zonation is a landscape-wide conservation priority classification based on the complementarity of various input geospatial layers, determining optimal site selection for multiple variables (Moilanen et al., 2011, 2005). The priority ranking is determined by continuously eliminating the grid cell or planning unit with the smallest aggregate loss of conservation value, and accounts for the species distributions, assigned weights and connectivity of features. In the case of infrastructure, this permits the elimination of extremely poor landscape areas prior to further iterative cell removal (Moilanen, 2007) or a region threatened by future development could be negatively weighted to preferentially select other areas (Moilanen and Arponen, 2011). For all features, the exponent of the power function was set to $z = 0.25$. The allocation of weights to features in Zonation has a significant impact on the distribution of importance among the various features in the prioritization solution. Furthermore, negative values may be assigned to weights in certain cases, such as when numerous opportunity costs are incorporated into the analysis, such as for infrastructure or land costs, as shown by Di Minin et al. (2013) and Moilanen et al. (2011). To avoid unequal weights based on the corridor connectivity features, we assigned the same aggregate weight to each of the corridor models ($W_j = 1$). In the infrastructure overlays, the pollution features were included as negatively weighted features ($W_j = -1$). The landscape integrity layer was included as a condition. These features enable the weighting and ranking of areas that are most vulnerable to development, as well as areas that are most important for maintaining biodiversity.

Prioritization tools are also used to identify areas based on their ecological value and can perform scenario-based analysis. We developed several scenarios: i) baseline corridor connectivity, a scenario where the corridors and current 2019 baseline infrastructure were included in the analysis, and ii) future development scenarios – Florida 2040 and Florida 2070 development including urban sprawl and conservation projection alternatives.

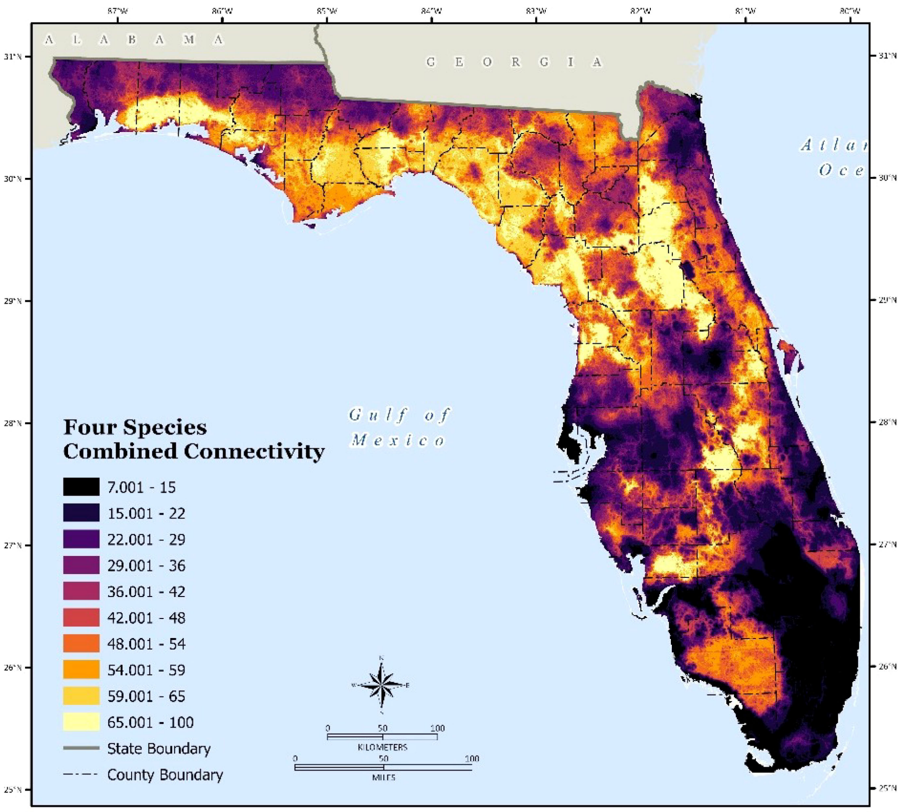
Results

Integrated combined models

The landscape connectivity models for Linkage Mapper (Supplementary Information 2 - Figure S2), Omniscape (Supplementary Information 2 - Figure S3), and resistant kernel (Supplementary Information 2 - Figure S4) were output for each species. Models for a combined three model species-specific connectivity output were also calculated (Supplementary Information 2 - Figure S5). Finally, we integrated the multi-model combinations for the species together for an integrated combined connectivity approach: Florida panther, Florida black bear, eastern indigo snake and southern fox squirrel (Figure 1).

Correlation coefficients

The Florida panther and Florida black bear showed significant levels of overlap (correlation 0.77) in their habitat preferences, with more broad levels of suitable connectivity throughout the landscape. We also found some correlation between eastern indigo snake and southern fox squirrel connectivity (correlation 0.375) (Table 2), Florida black bear and eastern indigo snake (correlation 0.312), Florida panther and southern Fox Squirrel (correlation 0.241). There was little overlap for connectivity models between Florida panther and eastern indigo snake (correlation 0.078) or Florida black bear and southern fox squirrel (correlation 0.11).



Date: 9/2023. Data: Environmental Systems Research Institute, Florida Department of Agriculture and Consumer Services, Florida Fish and Wildlife Conservation Commission, Florida Geographic Data Library, Florida Natural Areas Inventory, University of Florida Center for Landscape Conservation Planning, U.S. Census Bureau, U.S. Geological Survey. Projection: Albers Conical Equal Area

FIGURE 1
Integrated combined connectivity for the four focal species: Florida panther, Florida black bear, eastern indigo snake and southern fox squirrel.

Conservation implications

Our results for the top 10 and 20 percent of corridor connectivity were overlaid with the Florida conservation lands and the Florida Wildlife corridor blueprint for priorities 1-3 (Figure 2).

Bottleneck and pinchpoint mapping

Our goal was to illustrate the subset region characterized by a significant but unprotected prospective multispecies connection corridor and show each target species' mobility bottlenecks or constricted movement (Figure 3). The Florida panther and Florida black bear had more constricted bottlenecks and flow obstruction in southern Alachua County, while the southern fox squirrel and eastern indigo snake had less, likely due to their scarce occurrence records and the pinchpoints being more defined between smaller suitable patch occurrences. Although with fewer corridors and potential for movement, the eastern indigo snake was modeled as having the most restricted movement across the landscape; therefore, bottleneck areas are located within those restricted areas.

Spatial conservation prioritization

Our results from including the Zonation rankings further emphasize the existing infrastructure and threats to the landscape (S3). Full statewide maps are available (Supplementary Information - Figure S6), in addition to the study area subset in north central Florida centering on Alachua county (Figure 3).

Discussion

A growing amount of research shows that wildlife corridors should incorporate multi-species connectivity to retain key ecological processes over wide geographic regions (Koen et al., 2014; Brodie et al., 2015; Dilkina et al., 2017; Riggio et al., 2022; DeMatteo et al., 2023). We have identified a common corridor map among multiple species using the most reliable statewide species occurrence information, habitat suitability data, and connectivity modeling. These methods may be used to supplement the existing geospatial data layers in FEGN planning and prioritization to include additional and more specific metrics of connectivity for species of conservation importance to the state.

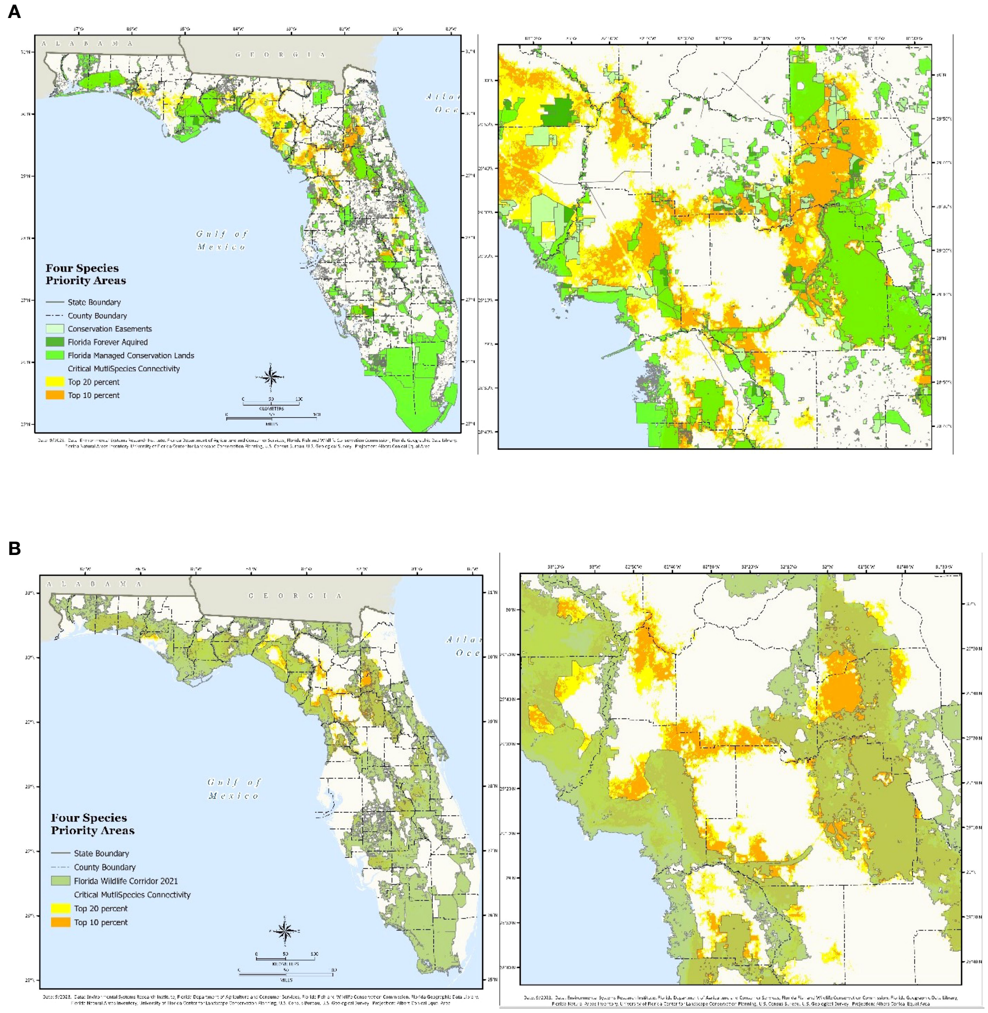


FIGURE 2
The top 10 and 20 percent of the four species connectivity modeling results with overlays for statewide (left) and southern Alachua County and O2O corridor (right) for **(A)** protected Florida conservation lands and **(B)** Florida Wildlife Corridor plans.

Combining the results of these various models at the regional scale was a crucial component of our strategy to leverage the results. The various landscape connectivity models enabled us to incorporate the strengths of various methodologies. The Linkage Mapper analysis provided predictions of the most suitable corridors that could be constructed between the patches defined for each species. The resistant kernel analysis provided predictions of biologically meaningful dispersal distances from core habitats. The Omniscape analysis provided predictions across the landscape for a pixel-by-pixel circuit theory-based model for connectivity. Finally, we combined the map quantiles of these three approaches into one combination map for each species to leverage the strengths of the three models. Similar multi-model efforts have been made to apply ensemble modeling to machine learning algorithms (Fox et al., 2017; Dondina et al., 2020), and model averaging (Dormann et al., 2018) to the problem of determining habitat suitability for a particular species, but these techniques have not readily been transferred to the connectivity models currently in use. We sought to combine the models in a way that was simple and straightforward using map quantiles of the results for an equal weighting. The results revealed the most specific and optimal areas for conserving the four focal species. Since our study models connectivity specifically between the core habitat patches or occurrences using species-specific habitat suitability and by adding specific potential dispersal distances, more general landscape connectivity methodologies may reach a different result. The FEGN already uses a large collection of habitat suitability models, thus this research investigated the possibility to combine connectivity-related indicators using an integrated multi-model multi-species connectivity approach.

The modeling framework used in this study should improve upon previous modeling work to connect potential breeding habitats for Florida panthers and black bears to promote functional connectivity and gene flow. We sought to highlight the historical habitat fragmentation and patch isolation on the Florida panther population, including inbreeding and genetic drift (Johnson et al., 2010; Kerk et al., 2019; Saremi et al., 2019), along with the current limited range of the Florida panther population

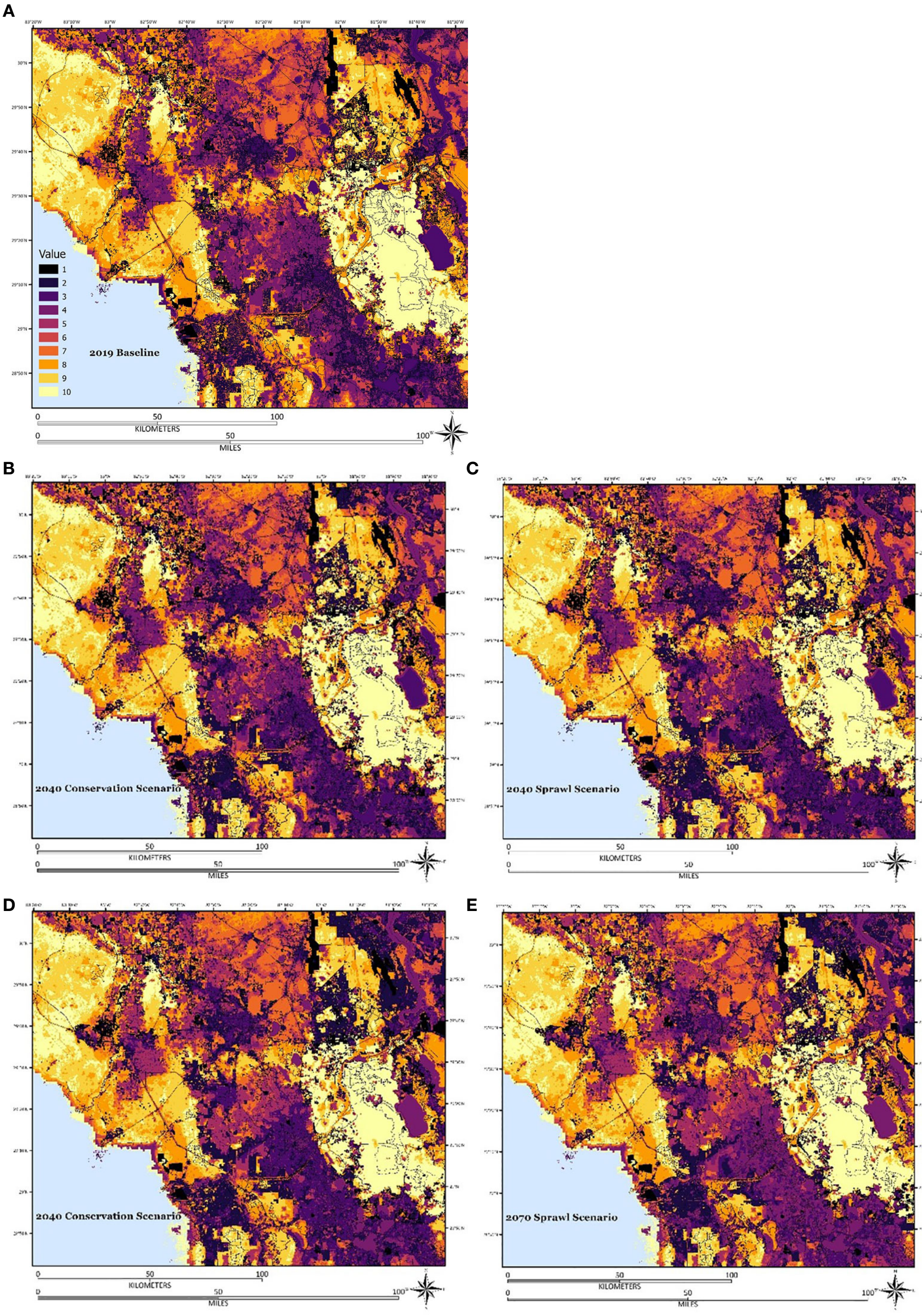


FIGURE 3
Spatial prioritization of future development, infrastructure, and threats for **(A)** 2019 development baseline, **(B)** 2040 conservation scenario, **(C)** 2040 sprawl scenario, **(D)** 2070 conservation scenario, and **(E)** 2070 sprawl scenario. Values represent areas of highest connectivity (10 yellow) and lowest connectivity (1 black) with the threats, pressures, and landscape integrity factored in.

(Hostetler et al., 2013) and the need for further efforts to facilitate population growth and remove the species from the endangered species list (Hedrick and Fredrickson, 2010; Johnson et al., 2010; Gustafson et al., 2019; Kerk et al., 2019; Saremi et al., 2019). Natural dispersal of females may not be a viable strategy for population expansion and translocations of females to establish new populations in central and northern Florida has been suggested (Maehr et al., 2002; Thatcher et al., 2009; Frakes and Knight, 2021). Understanding the prospective interconnectivity among reintroduction regions can provide valuable insights for endeavors aimed at long-term, practical ecological connectivity planning.

Results illustrate the potential for restricted movement of certain species in a specific study area. We found that the Florida panther and Florida black bear had larger levels of restricted movement compared to the southern fox squirrel and eastern indigo snake, likely due to the habitat patch suitability for each species being very different in size. We highlight the need for future research to prioritize specific pinchpoints for priority species to keep small patches connected within large landscape conservation efforts (see Figure 4). The ability to conserve smaller species at a statewide scale would require a finer scale prioritization and may assist in prioritization for adaptive management at the county or multi-county level scale as well. Although few papers have discussed the implications of pinchpoints in the design and prioritization of corridor planning, here we have illustrated pinchpoints based on the combination of two modeling methods. Our results highlight the importance of the Ocala to Osceola (O2O) Wildlife Corridor, which is currently a regional partnership led by the North Florida Land Trust. (https://o2owildlifecorridor.org/), for important habitat and restricted flow for the southern fox squirrel, eastern indigo snake, as well as long term restricted flow for Florida panther and black bear. Movement across land designated for future protection should attempt to safeguard places that may offer diffuse flow for wildlife or areas becoming progressively confined to prevent such channels from being entirely obstructed (Carroll et al., 2012; McRae et al., 2012). The strategic prioritization designs of the current FLWC do not account for pinchpoints, even though research has identified the necessity of identifying and validating pinchpoints. Future research may seek to understand the major pinchpoints throughout the state for these species based on the methods presented in this study and seek to use landscape design principles for effective pinch point prioritization. In addition, future strategic prioritization of the FLWC is intended to better incorporate consideration of pinchpoints and similar bottlenecks to further refine the identification of top priorities for closing functional gaps in protected corridors.

One of our objectives was to assess the effectiveness of multi-species connectivity relative to the FLWC and the Florida conservation lands portfolio. We were able to identify areas shared by all four species that were not protected by the current protected area estate nor the FLWC priorities 1-3, illustrating additional potential priorities for land acquisition. There were large areas of northern Florida that remain unprotected. One of

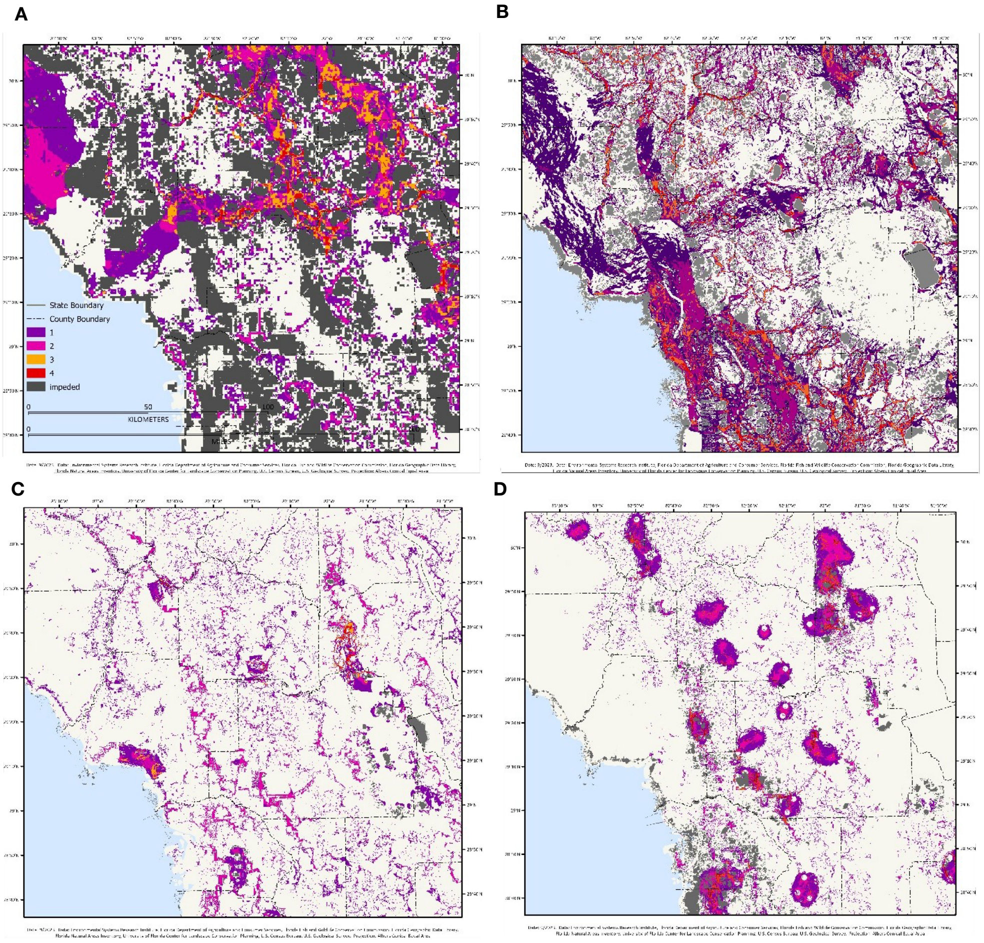


FIGURE 4
Pinchpoints and bottlenecks have been identified for the following species: **(A)** Florida panther, **(B)** Florida black bear, **(C)** eastern indigo snake, and **(D)** southern fox squirrel. Maps illustrate impeded flow (grey) as well as the pinchpoints ranked on a scale from 1-4 (with four being the most constricted).

TABLE 2 Correlation coefficients between the combined model outputs for the four focal species.

	Florida Panther	Florida Black Bear	Fox Squirrel	Indigo Snake
Florida Panther	–	0.776	0.241	0.078
Florida Black Bear	–	–	0.110	0.312
Fox Squirrel	–	–	–	0.375

the main areas based on our analysis was Putnam, Marion, and Clay counties, in the O2O wildlife corridor (Figure 2). Other counties that have protection gaps included Alachua, Levy, Gilchrist, Dixie, Taylor, and Lafayette counties. We highlighted this with several maps further investigating this subset for protection with a Zonation approach (Figure 3). The corridor connectivity in our subset study area around southern Alachua County illustrated the potential for identifying and protecting connectivity for the four focal species, while also revealing underlying factors such as infrastructure, landscape integrity, and future development on the area that likely further degrade connectivity due to human pressure and loss of landscape integrity.

For the purposes of planning and prioritizing spatial conservation, additional considerations are made regarding land acquisitions, such as pollution sources and other potential threats. Future designs of the FLWC may be significantly influenced by the implications of large-scale infrastructure, which is why the FLWC is iteratively updated to incorporate threats as land use changes. To assess methods or increasing priority of areas with higher potential threats, additional research is required to ensure all elements of built infrastructure that might impede ecological connectivity are fully considered. Our work shows the potential impact of including more thorough built infrastructure in ecological connectivity planning but needs additional refinement to fully integrate existing and future threats in strategic prioritization. As the results of our Zonation model indicate, we attempted to depict interconnected regions that are presently less impacted by pressures or threats from human activity, highlighting refugia from multiple stressors of human activity.

Major transportation corridors and the built environment were listed by experts as among the greatest threats to the Florida Wildlife Corridor and multi-species habitat connectivity. At present, ten under-construction or proposed major expressways and toll roads of statewide to regional scope are part of the work programs in the Central Florida Expressway Master Plan 2045 and the Florida Transportation Plan 2045, and assessing, avoiding, and fully mitigating the impacts of future highway construction is essential for effective ecological connectivity planning. Road networks in south Florida have disrupted the panther's habitat (Schwab, 2006), separating the sexes and reducing mobility of females more than males (Schwab and Zandbergen, 2011). Fragmented habitats also result in larger home ranges for animals, such as bears, as they avoid urban areas and major roads (Karelus et al., 2019, Karelus et al., 2016). Lack of conservation and connectivity among bear subpopulations can worsen habitat fragmentation and threaten population stability (Poor et al., 2020). Studies recommend building underpasses to protect Florida black bears from ever increasing road density and vehicle traffic that negatively affect adult survival and are the leading cause of mortality for bears and other large carnivore populations (Hostetler et al., 2009). Pressure and changes in land use patterns are also anticipated to occur during the horizon of our models, illustrating how conservation related scenarios of development will influence future land-use patterns in 2040 and 2070. This information could help safeguard statewide and regional connectivity of the populations of all four focal species and maintain genetically diverse populations through immigration and emigration if it is used to ensure and protect functional ecological connectivity before projected habitat loss to development occurs.

Limitations

Our study served as an example of a potential workflow to integrate multiple species and multiple models into landscape conservation planning. There are more species of importance that we have yet to include in this work that will likely influence future results. We chose two wide-ranging carnivores (Florida Black Bear, and Florida Panther), one large snake and one small mammal with regional landscape to landscape scale habitat needs and dispersal capabilities. Our goal moving forward is to integrate additional priority species into this workflow including wood stork (*Mycteria americana*), flatwoods salamander (*Ambystoma cingulatum*), swallow-tailed kite (*Elanoides forficatus*), gopher tortoise (*Gopherus polyphemus*), red-cockaded woodpecker (*Leuconotopicus borealis*), short tailed hawk (*Buteo brachyurus*), Florida scrub jay (*Aphelocoma coerulescens*) and a revised layer for xeric connectivity related species. Florida is home to myriad species that, despite an abundance of data, are not necessarily considered priorities by the state due to their conservation status as common or least concern species where maintaining connectivity would be considered a low priority compared to more urgent priorities. The challenge is to adequately rank species priorities in the final FEGN data products. The FEGN now includes 12 species' habitat suitability maps, where the goal is to continue to integrate additional connectivity related data layers of more species to further improve identification of priority areas of habitat connectivity.

Future research

Using multiple models, we would hope to increase the potential for model validity, although without on-the-ground validation the benefits of multi-model efforts compared to single model efforts are currently unknown. Future work is needed to validate these models with on-the- ground data, such as a separate data collection effort, e.g., road mortality data (Iverson et al., 2024). Particularly for at-risk species and natural communities that are frequently data deficient due to the absence of formal data collection efforts, be it independently collected, or even through citizen science programs, validating multispecies models would be a challenging endeavor. Frequently, the data accessible via portals like the Global Biodiversity Information Facility (GBIF) are identical to the data accessible via NatureServe and the Florida Natural Areas Inventory programs; thus, they lacked independence from the underlying data and models used in our study. Furthermore, these datasets are frequently skewed toward common species within the state or comprise citizen science data that may not meet the criteria for research quality for priority at-risk species. Independent validation for single species models has been explored in separate research for Florida black bear using GPS collaring data, focusing on the use of various resistance surfaces making a large difference in effectiveness of the models (Poor et al., In Review)[1]. There are road mortality data available for Florida black bear and Florida panther, although for the Florida panther, the statewide scale of our models does not match the location of mortality data given that current movement for panthers is concentrated primarily in south Florida, with only occasional documented movements further north. Finer scale validation efforts would be necessary to produce the type of robust validation of multiple species crucial to corridor linkages identified in this study.

Future research may seek to integrate a dynamic connectivity approach that also includes future scenarios in the underlying habitat suitability models to see how connectivity shifts, including climate-wise connectivity for climate adaptation planning in addition to future development threats (Jennings et al., 2020a). A wide array of species and habitats are imperiled by climate change, sea level rise, and land cover transformation in Florida, where further research is needed to identify spatial priorities using long term datasets. Additionally, future extensions of this research may seek to integrate spatially explicit population modeling to better understand how the modeled connectivity planning would currently enable or hinder population growth for certain species within these new land mosaics of planned development.

Conclusions

Conservation techniques must adapt to Florida's suburban development, which is negatively altering species ranges and ecological dynamics, and find ways to preserve functional connectivity in quickly changing landscapes. Our study simulated movement for four focal statewide species: the Florida panther, Florida black bear, eastern indigo snake, and southern fox squirrel. Our research aimed to use the results of different landscape connectivity models based on circuit theory and least-cost corridors to assess possible conservation areas for the protection of connectivity and to identify priorities for the FEGN/FLWC. The models utilized resistant kernels, least cost corridors, and Omniscape modeling to simulate the movement throughout Florida. Our research shows that conservation strategies that focus on limited, single species applications may prove inadequate for all species on account of variances in habitat suitability, dispersal distances, home ranges, and susceptibility to human activities, necessitating a multispecies approach. Our research also assessed the effectiveness of the existing protected area extent in maintaining connectivity for these species, as well as the capability of the FLWC to address their requirements and found a few significant gaps that should be considered in future protection strategies. Additionally, we investigated a subset of our study area in north central Florida, centered on Alachua County, of constricted species movement through the analysis of bottlenecks and impedance zones for a subset of the study area, finding that the larger mammals (Florida panther and Florida black bear) showed higher levels of constricted and impeded flow in larger areas, with smaller animals (eastern indigo snake and southern fox squirrel) having smaller pinchpoints between smaller occurrence patches, highlighting the need for a finer scale prioritization. Furthermore, we incorporated expert opinion rankings of infrastructure and threats using the spatial conservation prioritization software Zonation. This analysis developed a landscape integrity-based assessment of connectivity modeling using a baseline for infrastructure development in 2019, as well as alternative 2040/2070 future development scenarios. For prospective long-term protection of a subset of the southern Alachua County connection, the results of the analysis demonstrated loss of landscape integrity at the regional scale, as well as gaps in connectivity for both existing conservation status lands and the FLWC, while still highlighting the potential for more effective multi-species conservation in the region.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

EB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. JO: Data curation, Investigation, Project administration, Writing – review & editing. RN: Conceptualization, Supervision, Writing – review & editing. MO'B: Data curation, Investigation, Writing – review & editing. RF: Data curation, Investigation, Writing – review & editing. DS: Investigation, Methodology, Writing – review & editing. SL: Writing – review & editing. JM: Data curation, Writing – review & editing. BS: Data curation, Writing – review & editing. EP: Data curation, Writing – review & editing. TH: Writing – review & editing.

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[1] Poor, E., Schieck, B., Cox, J., Guthrie, J., and Mullinax, J. (In Review). Towards robust corridors – a novel validation framework to more efficiently create corridors.

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Conflict of interest

Author RN was employed by Conservation Science, Inc.

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1406944/full#supplementary-material

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RE-ARMing salt marshes: a resilience-experimentalist approach to prescribed fire and bird conservation in high marshes of the Gulf of Mexico

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Uncertainty, complexity, and dynamic changes present challenges for conservation and natural resource management. Evidence-based approaches grounded in reliable information and rigorous analysis can enhance the navigation of the uncertainties and trade-offs inherent in conservation problems. This study highlights the importance of collaborative efforts and evidence-based decision-making, specifically implementing the Resilience-Experimentalist school of adaptive management (RE-ARM), which emphasizes stakeholder involvement, shared understanding, and experimentation. Our goal was to develop an adaptive management framework to reduce the uncertainty around the use of prescribed fire to manage the habitat for eastern black rails (*Laterallus jamaicensis jamaicensis*) and mottled ducks (*Anas fulvigula*) in saltmarshes of the Gulf of Mexico. Supported by discussions at a series of workshops, we used a value of information analysis to select a fire management hypothesis to test, developed an influence diagram to represent the system under fire management, used the influence diagram to develop a Bayesian decision network (BDN), and conducted a power analysis to guide management experiments and monitoring. Value of information analysis identified fire return interval as the critical uncertainty. Our BDN provided valuable insight into how managers believe prescribed fire influences vegetation characteristics and how vegetation influences both eastern black rail occupancy and mottled duck abundance. The results of the power analysis indicated that a standard occupancy modeling framework was more useful to compare 2- and 5-year fire return intervals for black rails than two alternative designs (removal and conditional). Our BDN can be used to predict the probability of achieving the desirable vegetative response to increase the occupancy probability of black rails and abundance of mottled ducks, and monitoring data can be used to update the BDN (learn) and improve best management practices for prescribed burns (adapt). Linking the value of information, BDNs, and power analysis enhances our understanding of the system, improves management decision-making, and builds trust among scientists, interested parties, and decision-makers. This approach lays the groundwork for knowledge co-production and adaptive management.

KEYWORDS

adaptive management, Bayesian decision network, co-production, marsh birds, power analysis, structured decision making, value of information

1 Introduction

Conservation and natural resource management decisions are characterized by uncertainty, complexity, and dynamic change. A multitude of stressors, such as habitat loss and fragmentation, climate change, and disease, pose significant threats to wildlife. These threats are often interconnected, and their impacts can compound in unpredictable ways (NASEM, 2022), further exacerbating the challenges faced by wildlife populations (Polasky et al., 2011; Game et al., 2014). Evidence-based conservation approaches enable us to navigate the uncertainties, trade-offs, and conflicting interests inherent in these problems, ensuring that management efforts are grounded in reliable information and rigorous analysis (Nichols, 2012; Salafsky et al., 2019; Fuller et al., 2020).

Effectively tackling conservation and natural resource management issues is benefitted by collaborative efforts (Beier et al., 2017; Cundill and Fabricius, 2009; Dubois et al., 2020). Adaptive resource management (ARM; Lancia et al., 1996) is a collaborative, iterative approach to decision-making and resource management that engages scientists, interested parties, and decision-makers and aims to address complex and uncertain problems. There are two primary schools of adaptive management: Resilience-Experimentalist (RE-ARM) and Decision-Theoretic (DT-ARM; McFadden et al., 2011). The DT-ARM framework is grounded in decision-theory and focuses on defining the management problem, objectives, and alternatives with no explicit requirement for experimentation to test management actions (McFadden et al., 2011; Johnson et al., 2013). An important difference between DT-ARM and RE-ARM is that DT-ARM often frames management as a Markov decision process with a single decision-maker and uses an optimization algorithm (e.g., stochastic dynamic programming) to provide a sequence of optimal decisions (Williams, 2009), whereas RE-ARM emphasizes a general learning process that embraces uncertainty and uses the principles of experimental design as part of “learning-by-doing” (Walters and Holling, 1990; Walters, 1997). Within the RE-ARM framework, emphasis is placed on early involvement by interested parties, experimentation to test management hypotheses, and evaluation of management outcomes to create a shared understanding of system dynamics among interested parties. The collaborative learning process of the RE-ARM framework leads to improved communication and trust among participants and experiments offer distinct advantages in establishing causality and providing strong evidence for making informed decisions (Gerber et al., 2020; Ockendon et al., 2021; Caro et al., 2023).

In the context of RE-ARM and DT-ARM, value of information (VOI) can be an important tool to identify which uncertainty, if resolved, will result in greatest management benefits (Walters, 1986; Yokota and Thompson, 2004; Runge et al., 2011; Williams et al., 2011). VOI analyses compare the expected outcomes of different management actions under uncertainty with expected outcomes after resolving uncertainty. By considering the potential effects of different actions and the uncertainties associated with each, managers can evaluate the sensitivity of management outcomes to different hypotheses (Williams and Johnson, 2015; Bolam et al., 2019). This comparison helps prioritize which management actions to test experimentally within the RE-ARM framework.

Bayesian decision networks (BDNs) provide a framework for representing and reasoning about uncertainty and for explicitly representing decision alternatives and their utilities (Marcot et al., 2006; Chen and Pollino, 2012). BDNs are constructed based on a conceptual model (i.e., influence diagram) that represents causal, logical, or other relationships among variables and their dependencies. BDNs can be easily created in participatory settings, particularly with experts contributing their knowledge, insights, and diverse perspectives, thereby improving the development process and parameterization of the network (Drew and Collazo, 2012; Hassall et al., 2019; Marcot, 2019). As new data are collected, the BDN can be repeatedly updated, refined, and calibrated to improve its accuracy and relevance to decision-making (Nyberg et al., 2006). Finally, BDNs can incorporate multiple types of uncertainty relevant for adaptive management: environmental variation, structural uncertainty, partial management control, and partial observability (Williams, 1997; Lyons et al., 2008).

Power analysis assesses the potential for learning by estimating the statistical power of a monitoring design (Anderson, 1998; Steidl and Thomas, 2001; Di Stephano, 2003). Insufficient sample size can result in low power, increasing the risk of type II errors (false negatives) where true effects are not detected. Power analysis can identify the minimum sample size required to achieve a desired level of statistical power (i.e., to detect a meaningful effect) and is amenable to nearly any analytical framework including BDNs, allowing decision-makers to allocate necessary resources. Power analysis provides a quantitative measure of the ability to detect effects in adaptive management experiments—by considering statistical power, decision-makers can communicate the level of confidence in the reliability of monitoring outcomes and the effectiveness of strategies aimed at reducing structural uncertainty. Because experimentation is a fundamental aspect of the RE-ARM framework, conducting power analyses becomes an important step during experimental design to ensure an adequate amount of data is collected to facilitate learning and reduce critical uncertainties.

Here we present a case study of the setup phase for a RE-ARM framework to actively learn about and improve fire management strategies for eastern black rails (BLRA; *Laterallus jamaicensis jamaicensis*) and mottled ducks (MODU; *Anas fulvigula*) (hereafter, focal species) in U.S. Gulf of Mexico salt marshes. ARM frameworks include two distinct phases: a setup phase in which key components are developed and an iterative phase in which the components are linked together in a sequential learning and decision process (Williams et al., 2007). Our focus was on understanding and managing a dynamic ecosystem that involves interacting factors, nonlinear dynamics, and multiple decision-makers. Through experimentation, we can continuously improve our understanding of the system, refine our decision-making processes, and strengthen the ability to manage effectively. By coproducing the framework with experts, decision-makers, and other interested parties, we can harness their insights, generate shared ownership over the management strategies, and improve conservation for our focal species in the Gulf of Mexico. Throughout our case study, we show how coproduction tools from decision analysis, modeling, and monitoring can create a consortium for developing and improving evidence-based decision-advisory tools (Nichols et al., 2019).

2 Methods

2.1 Study area and focal species

The history of fire in salt marshes of the Gulf of Mexico has been shaped by both natural and anthropogenic causes (Nyman and Chabreck, 1995). Historically, fire was predominantly a natural occurrence, ignited by lightning strikes. These fires helped control the growth of woody vegetation, promote nutrient cycling, and create a mosaic of vegetation patches with varying stages of succession. Native Americans also had a long history of utilizing fire as a land management tool. However, during the 20th century, widespread fire suppression policies were implemented across the United States, including the Gulf of Mexico, leading to changes in ecosystem dynamics and altered natural fire regimes. Whereas there is increasing recognition of the importance of managing fire in salt marshes for conservation purposes, the effects of prescribed fire on focal species of concern, such as eastern black rails and mottled ducks, through changes to vegetation structure and composition, are unknown (Mitchell et al., 2006).

Eastern black rails are small, secretive birds that inhabit coastal wetlands, including salt marshes, in the Gulf of Mexico (Conway, 2011; Watts, 2016). They prefer dense, tall grasses, typically occupying areas with high marsh vegetation, especially where it transitions to low marsh or wet meadows, which provides cover and foraging opportunities (Roach and Barrett, 2015). Mottled ducks inhabit a variety of coastal wetland habitats in the Gulf of Mexico, including salt marshes, prairies, freshwater marshes, and estuaries. They prefer shallow marshes with dense emergent vegetation, such as cordgrass, sedges, and bulrushes, which provides important nesting and foraging areas (Bonczek and Ringelman, 2021; Haukos et al., 2010). Eastern black rails are federally threatened (USFWS, 2020), and mottled ducks are a regionally important game species (Krainyk and Ballard, 2016), with both species co-occurring in saltmarshes throughout the Gulf of Mexico. The response of eastern black rails and mottled ducks to prescribed fire in terms of habitat suitability is not fully understood.

2.2 Value of information to prioritize uncertainty

Because co-produced science and adaptive management are collaborative- and partnership-driven, we first established a planning committee composed of decision analysts and research scientists to develop a framework that integrates diverse perspectives and expert knowledge into the decision-making process. The planning committee identified a larger multi-disciplinary team of interested parties and experts with a diversity of experiences and knowledge (prescribed fire, focal species, high marsh management, endangered species regulation, conservation, etc.) who were either decision-makers or who have an influential role within a decision-making organization. We invited these experts to an initial adaptive management virtual workshop (hosted in September 2020) where we framed the decision context and created influence diagrams to illustrate the relationships among management actions and ecological variables within the high marsh (Figure 1). Using influence diagrams allowed for communication of key uncertainties and development of multiple working hypotheses that specified a threat to the focal species, description of the demographic mechanism by which the focal species were affected, and identification of a management action that may reduce or eliminate the threat. We calculated the constructed value of information (CVOI; Runge et al., 2023), which prioritizes sources of uncertainty in management actions, such as regarding the use of prescribed fire to benefit the focal species (i.e., increase BLRA occupancy or MODU abundance). Grounded in the algebra of the expected value of perfect information (EVPI), CVOI uses ratio scales to decompose EVPI into a contribution representing the relevance of the uncertainty to the decision and a contribution representing the magnitude of uncertainty (Runge et al., 2023). CVOI scores elicited from experts were used to identify the

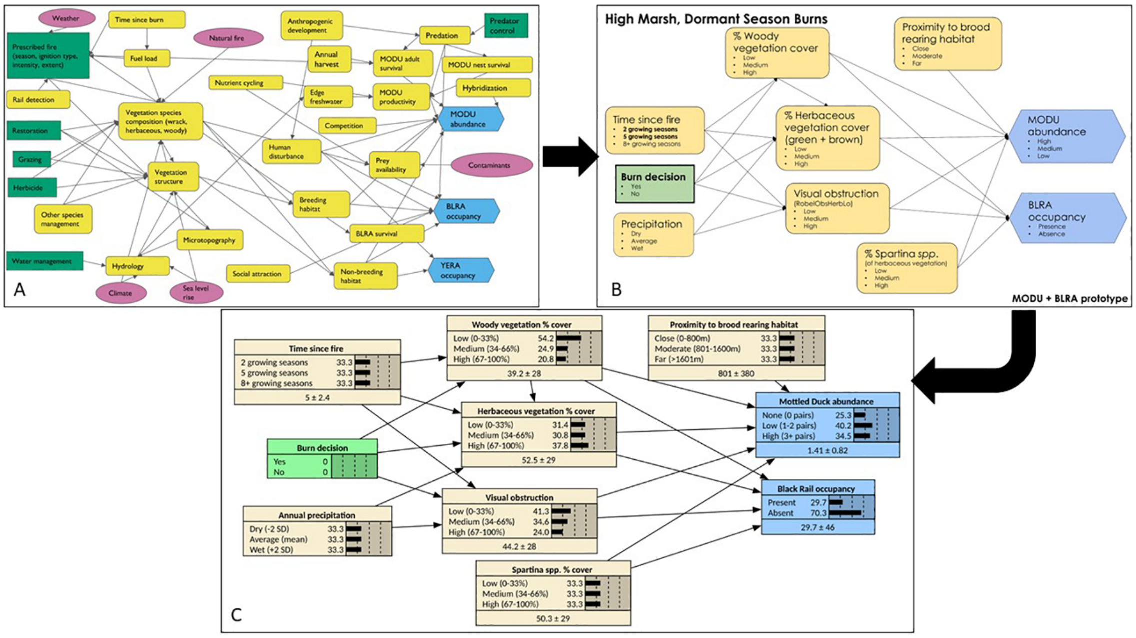

FIGURE 1
The progression from the original conceptual model **(A)**, developed during the initial adaptive management workshop, to a trimmed conceptual model **(B)**, where node states are defined for each component, and finally to a Bayesian decision network (BDN; **C**) parameterized with expert-elicited conditional probabilities tables. The initial conceptual model **(A)** was conceived as an influence diagram during brainstorming sessions in the early stages of the project. Green rectangles represent management actions, yellow rounded rectangles represent ecological variables, red ovals represent chance events, and blue hexagons represent fundamental objectives. Arrows represent the direction of cause and effect. The conceptual model was refined and streamlined **(B)** through an interactive and consultative process between subject matter experts and decision analysts. Specific states were assigned to each node for clarity and precision. The streamlined conceptual model **(B)** was transformed into a BDN **(C)**, incorporating expert knowledge through elicited conditional probabilities to quantify the relationships and uncertainties within the model. This progression highlights the evolution of the model from its conceptual inception to a fully specified BDN, enabling informed decision-making based on expert input and probabilistic reasoning.

hypothesis which, if tested, would best maximize management benefits (see Stantial et al., 2023 and Table 1).

2.3 Model development: Bayesian decision network

We followed the recommendations from Marcot et al. (2006) to convert the influence diagrams from the initial workshop into a BDN. The conversion process involves three steps: the alpha-level model, initially created from influence diagrams and expert judgment; the beta-level model, revised after peer review and calibrated with case data; and the gamma-level model, finalized by updating and validating with new data for final application (Marcot et al., 2006). We developed the BLRA alpha model in a second virtual model-building workshop (hosted in 2021), where our multidisciplinary team refined the BLRA influence diagrams, removed linguistic uncertainty among node definitions, converted the influence diagram to a BDN, and contributed values for the conditional probability tables (CPT; a table that represents the hypothesized influence of each parent node on the outcomes of child nodes; Stantial and Lyons, 2024) in the network via a formal elicitation for expert judgment (Hemming et al., 2018). Following the workshop, we averaged the individual experts' responses (Clemen and Winkler, 2007) and entered the CPT values into the alpha-level BDN in Netica® (Norsys Software Corp., www.norsys.com). Simple averaging has been shown to work well in many cases, and in this case, the experts' opinions were closely aligned, making simple averaging an appropriate and effective method for aggregating the responses (Clemen and Winkler, 2007). In a subsequent meeting, we reviewed the alpha-level BLRA model with participants, each of the relationships were discussed, and the alpha-level BLRA model was finalized. We procured two independent reviews from BLRA experts who reviewed the model structure and CPT values and confirmed the model's construction, which finalized the beta-level BLRA model. To create the gamma-level model, we conducted a one-way sensitivity analysis by varying one input node at a time while keeping the other input nodes constant (Conroy and Peterson, 2013). This allowed us to observe and measure the effect on the probability distribution for BLRA occupancy, evaluate the behavior of the BLRA BDN, and verify that the model's predictions were reasonable and informed.

We followed the same process to develop the MODU BDN, again, using the guidelines from Marcot et al. (2006). We then combined the gamma-level BLRA and MODU models into a single BLRA + MODU BDN because they shared most of the same environmental forcing variables and so that we might most efficiently evaluate tradeoffs among various fire return intervals for the two species (Figure 1).

TABLE 1 Hypotheses generated during workshop breakout group discussions about reducing uncertainty around prescribed fire decisions for eastern black rails, and mottled ducks in high marsh habitats along the Gulf of Mexico, USA.

Hypothesis name	Null hypothesis (H_0)	Alternative hypothesis (H_A)
1. Microtopography	There is no difference in pyrodiversity at sites with low and high microtopography indices.	Pyrodiversity is greater at sites with high microtopography indices because low-elevation patches will remain moist and burn less severely, whereas higher-elevation patches will be more severely burnt.
2. Interspersion	There are no differences in focal species occupancy between units that are uniformly burned and units that contain a mosaic of burned and unburned areas.	Focal species occupancy is greater at units with a mosaic of burned and unburned areas because unburned areas provide refugia during fire and leave habitat on the landscape while burned areas recover.
3. Mixed seasonality	There are no differences in vegetative response to burns conducted during both the dormant and growing seasons when compared to burns conducted during only the dormant or growing season.	Vegetative response is better when both growing and dormant season burns are used because burns during the growing season control woody vegetation, whereas burns during the dormant season provide the appropriate herbaceous vegetation structure.
4. Predation	There are no differences in nest success and survival at infrequently and frequently burned marshes.	As a result of reduced vegetative cover, marshes that are managed with frequent prescribed fire provide less cover for predators.
5. Fall vs. winter	All focal species will have the same response to prescribed fire.	Focal species will have a different response to fire depending on the season the burn is conducted due to differences in life history traits.
6. Matched seasonality	There are no differences in vegetative response to burns conducted during the growing season when compared to the dormant season.	Fires during the growing season (at historical frequency) produce a better vegetative response than dormant seasons because burns during the growing season control woody vegetation.
7. Mixed management	There are no differences in vegetative response and microtopography to light grazing used with prescribed fire when compared to prescribed fire only.	The appropriate vegetative structure and microtopography for focal species is achieved through a combination of light grazing and prescribed fire.
8. Return interval	There are no differences in vegetative response to fire frequency across the region.	Vegetative response varies with fire frequency across the region due to differences in regional precipitation.
9. Mosaic burn	There are no differences in focal species occupancy between units that are uniformly burned and units that contain a mosaic of burned and unburned areas.	Occupancy is greater in units that contain a burned–unburned mosaic (greater pyrodiversity) because unburned areas provide refugia during fire and leave habitat on the landscape while burned areas recover.

Hypotheses are stated in terms of the null and alternative versions. Source: Adapted from Table 1 in Stantial et al. (2023). © Stantial et al. Originally published under a CC-BY-NC-ND 4.0 license.

Once the gamma-level BLRA BDN was created, we hosted an interactive scenario modeling workshop (hosted in 2022) where our multidisciplinary team, other researchers, and other managers received firsthand experience running BDN scenarios of their choice in Netica with the gamma-level BLRA BDN (i.e., influence runs of Marcot, 2012). Scenario modeling involves using the BLRA BDN to simulate various management scenarios and predict their outcomes, allowing participants to explore and evaluate different strategies. Before the workshop, all participants received a copy of the model and downloaded the software to their computer so that they could conduct influence runs, which involve using the model to analyze the effects of different variables on the outcomes. We also reviewed the MODU + BLRA BDN, explored its functionalities, discussed model outputs in terms of causal and diagnostic reasoning, and discussed future steps for utilizing this model in adaptive management.

Finally, because reducing uncertainty and learning from experimental management are hallmarks of RE-ARM, we also conducted a learning simulation study to demonstrate methods for learning with a BDN. We simulated 1,000 observations of data from each node in the gamma-level BLRA model using the bnlearn package (Scutari, 2010) in R (R Core Team, 2023) under the assumption that the 2-year fire return interval would result in highest BLRA occupancy; we focused on fire return interval because it was prioritized as the critical uncertainty for managers in our value of information analysis (Stantial et al., 2023). We chose the 2-year fire return interval for demonstration purposes only; we do not draw inference about BLRA occupancy from this analysis. Rather, we consider this simulation to be one possible outcome for this study and use the analysis only to demonstrate model updating and Bayesian learning via RE-ARM. With the simulated data, we updated the gamma-level BLRA model in Netica using the expectation maximization algorithm (Do and Batzoglou, 2008). The simulated data were arranged in a spreadsheet with columns corresponding to each node in the Bayes Net and each row representing a simulated outcome (Netica refers to such a spreadsheet as “case data”). Updating the model was accomplished using Netica’s facilities for parameter learning from case data, which calculates a new conditional probability table at each node, given the model structure and the new data. To evaluate differences in the initial and updated model, we compared (1) Netica belief bars for the time since fire node, (2) the mean and SD (assuming Gaussian errors) of expected value for time since fire, and (3) the prior and posterior distributions for fire return interval, all conditional on BLRA being present.

2.4 Power analysis for management experiments

We conducted power analyses to guide our sampling design and determine the number of sites and surveys at each site needed to ensure an acceptable level of variance by which to then confidently test the effects of various fire return intervals on MODU abundance and BLRA occupancy. Knowing that BLRA and MODU surveys would be completed simultaneously under the same study design, we focused our power analyses on BLRA, which is a rare and cryptic species and occupancy estimates are often inaccurate for rare and cryptic species (Tolliver et al., 2019; Guillera-Arroita et al., 2014, 2010). We simulated BLRA occupancy data assuming an average occupancy probability of 0.30 and detection probability of 0.10, which may be conservative. Mean occupancy probability for the Gulf coast region ranges from 0.09 to 0.75, and detection probability ranges from 0.11 to 0.28 (McGowan et al., 2020a; Butler et al., 2023). Using the framework from Specht et al. (2017), we evaluated various sampling designs (standard, conditional, and removal) and effect sizes (small, medium, or large; Cohen, 1988) to determine the power to detect a difference between the null (no difference between 2- and 5-year fire return intervals) and fire treatment (difference between 2- and 5-year fire return intervals) models. The standard design involves multiple visits to all sites, the removal design ceases visits after initial detection, and the conditional design focuses follow-up efforts only on sites where the species was detected initially, each optimizing resource use based on species detectability and rarity (Specht et al., 2017). According to Cohen (1988), small, medium, and large effect sizes correspond to standardized differences (d) of 0.2, 0.5, and 0.8, respectively, representing small detectable, moderate visible, and substantial noticeable differences between groups. These standardized differences, or effect sizes, measure the magnitude of difference between groups in a standardized way, allowing comparisons across different studies and variables (Cohen, 1988). Using the results of the power analysis, we finalized the sampling design through consensus among a small team of experts, who evaluated the implications of different study designs and power thresholds on our study's objectives and resource constraints. The study design will be used to guide the iterative phase of adaptive management.

3 Results

Using their influence diagrams, the participants generated nine management hypotheses at the initial workshop (Table 1; see also Table 1 from Stantial et al., 2023). The hypothesis with the greatest value of information for decision-making based on the results of the CVOI analysis was the Fire Return Interval hypothesis (Table 1, #8). This hypothesis was chosen for experimentation within a RE-ARM framework, aiming to expedite the learning process regarding the effects of fire frequency on the focal species.

During the second workshop, we finalized the BLRA conceptual model, converted the BLRA conceptual model into a BDN, and parameterized the BLRA BDN through expert elicitation to create the alpha-level BLRA BDN model (Figure 1). The alpha-level BLRA BDN comprised a burn decision node, six ecological variable nodes, one species occupancy node (Table 2), and the causal relationships among these components (as shown in Figure 1). The fully parameterized, alpha-level BLRA BDN was the average of the individual expert-elicited conditional probabilities (n = 20). The average probability of BLRA occupancy being present across all ecological states and management decisions from the expert-elicited conditional probabilities was 29.7%.

Through demonstrations and discussions during our interactive scenario modeling workshop, the attendees gained a thorough understanding of BDNs, the importance of various habitat variables on BLRA occupancy and MODU abundance, and the predictive capabilities of these networks in assessing the ecological impacts of varying fire frequencies on BLRA and MODU habitat. The participants also gained a thorough understanding of the practical application of BDNs in adaptive management.

During the final workshop, we focused on finalizing the MODU conceptual model, converted the MODU conceptual model into a BDN, and parameterized the MODU BDN through expert elicitation. The final MODU BDN was composed of a burn decision node, seven ecological variable nodes (six from the BLRA BDN and one specific to MODU), one species abundance node, and the causal relationships among these components (Table 2). The fully parameterized MODU BDN was the average (n = 19) of expert-elicited conditional probabilities. The mean probability of high MODU abundance was 25%, while low abundance had a mean probability of 40%, and none had a mean probability of 35%.

The results of our one-way sensitivity analysis with the gamma-level BLRA + MODU BDN suggested that the node most influential to BLRA occupancy was the herbaceous vegetation node whereas the annual precipitation node was the least influential (Figure 2A). The node most influential to MODU abundance was the proximity to brood rearing habitat whereas the annual precipitation node was the least influential (1.7%; Figure 2B). The learning simulation study explored a scenario in which BLRA are found most often in management units with a 2-year fire return interval. In the initial model parameterized with expert judgment, the belief bars for the time since fire node are nearly equal and reflect managers' uncertainty about the effect of fire return interval (Figure 3A). The mean time since fire in this model was 4.8 growing seasons (SD = 2.4). In the updated model, the belief bars are unequal and reflect evidence, as expected, that BLRA are found more often in the 2-year return interval (Figure 3B). The mean time since fire in the updated model was 2.8 growing seasons (SD = 1.3). The posterior distribution for time since fire (updated model) shifted as expected and showed smaller variance compared to the prior distribution (initial model; Figure 3C).

The results of the power analysis for BLRA occupancy revealed no differences between the standard, conditional, and removal sampling designs (Figure 4). We found that if the effect size is small, no matter the sampling design or number of surveys, we will have low power to detect a difference between the fire treatments. Our results suggest that if the effect size is medium or high, surveying 375 points (S) eight times (k) under the standard

TABLE 2 Bayesian decision network (BDN) nodes, node states, and definitions for the adaptive management BDN used to evaluate the effects of varying intervals of prescribed fire on eastern black rails and mottled ducks in the Gulf of Mexico.

Node	States	Definition
Eastern black rail (BLRA) occupancy	Present	The probability of the presence/absence of a black rail at a management unit
	Absent	
Mottled duck (MODU) abundance	None (0 pairs)	Number of indicated pairs at a survey point. Indicated pairs may be one or two individuals exhibiting breeding behaviors within a survey point. Indicated pairs are defined as single individuals observed in either drop flight or emerging from vegetation, which are behaviors suggestive of breeding OR two individuals observed together in either drop flight or emerging from vegetation.
	Low (one to two pairs)	
	High (3+ pairs)	
Proximity to brood rearing habitat	Close (0–800 m)	Euclidean distance to the nearest MODU brood rearing habitat (as measured with remotely sensed data from the point count location)
	Moderate (801–1,600 m)	
	Far (>1,601 m)	
Herbaceous vegetation	Low (0%–33%)	Proportion of the management unit (as measured by quadrat and averaged across plots) covered by both green and brown herbaceous vegetation (the remainder of the quadrat would be a combination of bare ground and woody vegetation)
	Medium (34%–66%)	
	High (67%–100%)	
Visual obstruction	Low (0–30 cm)	Height of complete visual obstruction of herbaceous vegetation (as measured using a Robel pole, from the bottom of the pole, the first bin that is not 100% covered by herbaceous vegetation)
	Medium (31–60 cm)	
	High (60+ cm)	
Spartina spp.	Low (0%–33%)	Proportion of the herbaceous vegetation cover that is the combination of *Spartina patens*, *S. bakeri*, and *S. spartinae*
	Medium (34%–66%)	
	High (67%–100%)	
Woody vegetation	Low (0%–33%)	Proportion of the management unit (as visually estimated at the plot level) that is covered by woody vegetation (the remainder of the plot would be a combination of herbaceous vegetation and bare ground)
	Medium (34%–66%)	
	High (67%–100%)	
Time since fire	Two growing seasons	Number of growing seasons since fire was applied to the management unit
	Five growing seasons	
	8+ growing seasons	
Annual precipitation	Dry (-2 standard deviations)	Average annual precipitation as measured at the regional level by local weather stations
	Average (mean)	
	Wet (+2 standard deviations)	
Burn decision	Yes	Whether or not the management unit was burned during the previous dormant season
	No	

(Continued)

TABLE 2 Continued

The data for the conditional probability tables of each node were derived from expert elicitation (Stantial and Lyons, 2024).

sampling design, we will have a high power (>75%) to detect a difference between the null and fire treatment models.

4 Discussion

Our value of information (VOI) analysis identified that reducing uncertainty about the effect of fire return interval will provide the greatest management benefit to BLRAs and MODUs in high marshes of the Gulf of Mexico. Addressing the remaining uncertainty could help managers better understand ecological processes, balance the trade-offs between species, allocate resources more efficiently, and prioritize areas for burning—for example, burning too frequently may be counterproductive because vegetation might not have time to recover, leading to increased rates of soil erosion; however, not burning frequently enough might reduce habitat quality by leading to woody vegetation encroachment that provides little structural cover for the focal species. Regular, well-timed prescribed fires can sustain the diverse vegetation relying on these fire-adapted ecosystems, especially in the high marsh (Allain and Grace, 2001; Lynch, 1941; Nyman and Chabreck, 1995). Relative to the other hypotheses, the Fire Return Interval hypothesis was considered the most pertinent because it addressed a fundamental aspect of habitat management with high potential for improving ecological understanding and practical management outcomes for the focal species in Gulf of Mexico high marshes.

BDNs offer multiple advantages as a modeling framework for adaptive management. In our case study, BDNs allowed us to intricately map and analyze the complex interactions between fire management (fire return intervals), habitat variables, and BLRA occupancy and MODU abundance. Their graphical nature, with boxes and arrows showing influence, is intuitive, improving communication during co-production because participants with a wide variety of knowledge, insights, and perspectives can more clearly define, visualize, and discuss variables and their dependencies (Carriger and Newman, 2012; Robinson and Fuller, 2017). In this case, the participants were able to gain a thorough understanding of the complex relationships between management actions and ecological components of Gulf of Mexico high marshes through a hands-on learning demonstration of the BDN. It is also possible to parameterize a BDN with formal elicitation of expert judgment when data are lacking (Drew and Collazo, 2012; Marcot,

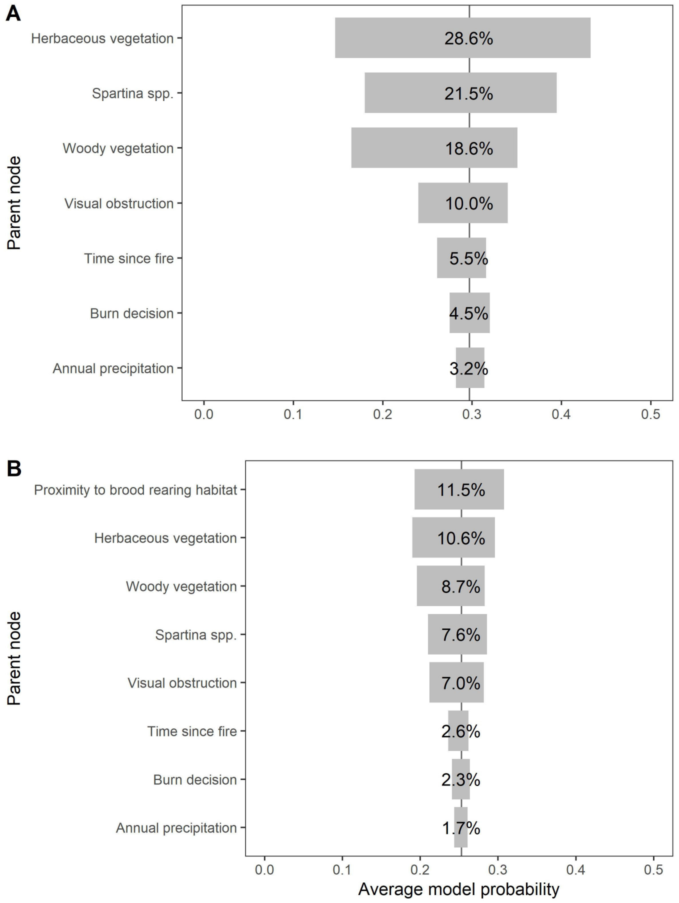

FIGURE 2
One-way sensitivity analysis depicting the sensitivity of the eastern black rail (BLRA) occupancy **(A)** and mottled duck (MODU) abundance **(B)** nodes to changes in their respective parent nodes within the Bayesian decision network (BDN). This analysis illustrates the extent to which variations in the parent nodes influence the outcomes of BLRA occupancy and MODU abundance, providing insights into the relative sensitivity of these key nodes in the BDN. Vertical lines in both panels indicate average model probability for BLRA presence (0.297) and high MODU abundance (0.253). The horizontal bars represent the maximum and minimum values when manipulating the parent node (y-axis) of the BDN.

2012; Hassall et al., 2019); the expert elicitation of conditional probability tables for the Gulf of Mexico BDN allowed a diverse set of experts to contribute their expertise, facilitating shared ownership of the modeling effort. As new data are collected, the BDN structure and probability parameters can be iteratively updated, refined, and calibrated to improve its accuracy and relevance to decision-making (Nyberg et al., 2006). Finally, resilience thinking places high value on understanding consequences of uncertainty for system behavior and management outcomes (Chapin et al., 2009; Polasky et al., 2011). Our BDN incorporates multiple types of uncertainty important for adaptive management (Williams, 2009; Lyons et al., 2008). First, the probabilistic relationships between the burn decision node and vegetation (child) nodes can help managers reduce uncertainty from partial management control; a burn decision does not always result in the same vegetation conditions, and as the CPTs for the vegetation nodes evolve over time based on field data, managers could gain insight about management control. Second, uncertainty related to environmental variation, while not reducible, is incorporated in the BDN with the precipitation node. Third, structural (model) uncertainty, including parametric uncertainty, can be understood and reduced over time via learning from case data and structural learning algorithms, e.g. those available in the R package bnlearn (Scutari, 2010).

Power analysis is a foundational component to any adaptive management program because it determines the sample size needed to detect statistically significant differences between models, guiding efficient resource allocation and ensuring that monitoring efforts yield reliable data (Williams et al., 2007). Our finding that there is no difference between standard, conditional, and removal sampling designs helps streamline the monitoring process by indicating that the typical, standard sampling design may be as effective as other designs. This is particularly advantageous because, at all of our survey locations, we will also be surveying for mottled ducks. Given the challenges of detecting BLRA, if one of the sampling designs had shown a substantial advantage in power to detect differences, we might have considered adapting our approach to accommodate that design. However, since none of the designs offer a significant advantage, it is more efficient and practical to use the standard sampling design for both species, allowing us to survey for mottled

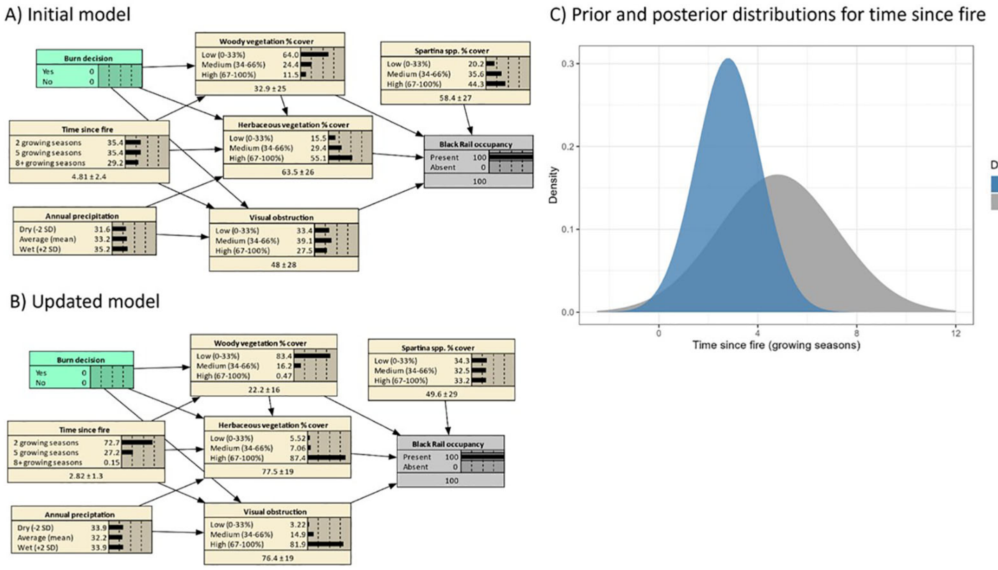

FIGURE 3

Learning (reducing uncertainty) about fire management with a Bayesian decision network (BDN) for eastern black rails. **(A)** The initial BDN parameterized with expert judgment shows high uncertainty about the effect of time since fire when eastern black rails are present (nearly equal belief bars for two, five, and 8+ growing seasons in time since fire node). **(B)** In the updated model after learning from simulated monitoring data, the belief bars reflect accumulating evidence that BLRAs prefer a fire return interval of two growing seasons (demonstration purposes only). **(C)** Prior (initial model) and posterior (updated) distributions for time since fire conditional on rails being present. The reduction in uncertainty (learning) is evident in the shift of the distribution and smaller standard deviation.

ducks and black rails at the same sites using the same sampling design. The identification of a threshold effect size for detecting meaningful differences underscores the necessity of designing studies with sufficient power. If the effect size is low, a much larger sample size will be necessary to reliably discern between the effects of 2- and 5-year fire return intervals. Therefore, power analysis has been critical to ensuring that the design of our experiment is robust enough to identify differences between fire return intervals that are meaningful for management decisions.

We parameterized the BDN for BLRAs and MODUs using expert elicitation, gathering conditional probability estimates from a panel of experts. The resulting parameterized BDN represented the mean expert-elicited conditional probabilities. Notably, the probability of BLRA being present, as derived from the expert data, was 30%. This finding closely aligns with published literature for Gulf of Mexico BLRA, where the average occupancy is reported to be around 30% (Tolliver et al., 2019). Such agreement between the expert-elicited data and the literature values is encouraging, indicating that the panel of experts provided reasonable and informed estimates for the conditional probability tables for each of the nodes in our BDN. This agreement not only validates the value of expert elicitation in parameterizing BDNs but also underscores the value of integrating expert judgment with empirical data to enhance the accuracy and reliability of modeling efforts (O'Hagan et al., 2006; Martin et al., 2012).

Implementation of adaptive management, whether RE-ARM or DT-ARM, includes two phases: a setup phase to identify key components and an iterative phase in which the components are linked together in a sequential learning and decision process (Williams et al., 2007). Our RE-ARM setup phase created the framework for collecting and analyzing data to reduce multiple types of uncertainty about the effect of prescribed fire in high marsh ecosystems. As our RE-ARM setup phase concludes, the iterative phase will allow for refining and adapting management strategies based on new knowledge, monitoring data, and interested parties' input. Data collected during the iterative phase can be readily incorporated into the BDN (Nyberg et al., 2006), enabling us to improve the model outputs, gain insight into system dynamics, and evaluate the effects of different fire return intervals on the focal species (i.e., learn). In other words, the iterative phase involves updating the model based on the collected data, laying the foundation for evidence-based decision-making in the future. As new knowledge about system dynamics accrues over time, it may be helpful to revisit the objectives, actions, and BDN as part of a "double-loop learning" process (Williams and Brown, 2018; McGowan et al., 2020b). Through double-loop learning, continuous improvements can be made, contributing to the conservation of the focal species and restoration of ecological balance within Gulf of Mexico high marshes.

Collaborative model co-production with participants was critical to improving the overall understanding of our data collection and helped to identify additional state variables of interest in our model. Participatory modeling thus resulted in robust monitoring protocols, ensuring that our data collection methodologies aligned with the hypotheses they are meant to inform. Moreover, the model-building process identified additional monitoring endpoints for "umbrella

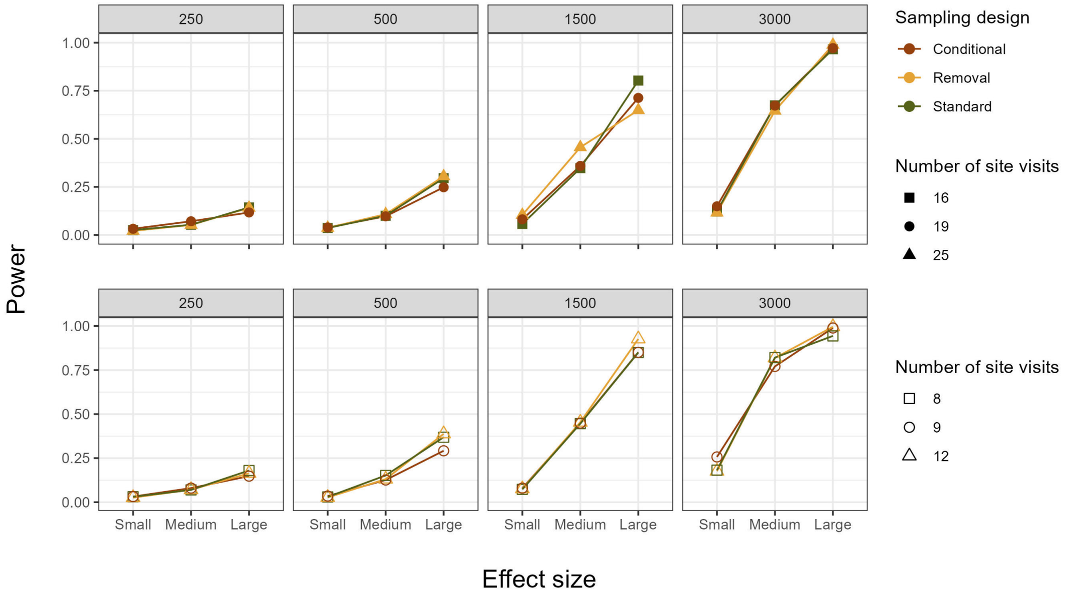

FIGURE 4
Power analysis for three different sampling designs for monitoring eastern black rail occupancy. The panels (gray bars at the top) represent total effort (number of surveys across all sites). Power to detect the fire treatment effect (y-axis) was estimated across different standardized effect sizes (x-axis) categorized as small (0.2), medium (0.5), and large (0.8) according to Cohen (1988). The shapes indicate the number of site visits (*k*) required. The top row represents the optimal number of surveys from Specht et al. (2017) (i.e., the number of survey repetitions at each site that will maximize the accuracy and precision of occupancy and detection probability estimates, based on the expected occupancy and detection probabilities), and the bottom row represents half the optimal number of site visits (half optimal = *k*/2). Additionally, sampling designs are represented by different colors.

learning," where auxiliary data collected during the iterative phase could also be extended to test other hypotheses. This collaborative strategy, driven by the co-creation of models and monitoring (Nichols, 2012; Nichols et al., 2019), has allowed valuable insights for our conservation and resource management initiatives for the focal species in this study.

Protecting species and restoring ecosystems necessitates informed decision-making based on reliable scientific knowledge. This study underscores the value of evidence-based decision-making in addressing the biodiversity crisis and highlights the importance of tools such as VOI analysis, BDNs, and power analysis in a RE-ARM framework to produce reliable and actionable science for adaptive management.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: https://www.sciencebase.gov/catalog/item/66a14f72d34ec831f2c2b50c (Stantial and Lyons, 2024).

Author contributions

MS: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. AF: Funding acquisition, Investigation, Supervision, Writing – review & editing. AL: Conceptualization, Investigation, Methodology, Writing – review & editing. BM: Methodology, Validation, Writing – review & editing. MW: Funding acquisition, Investigation, Supervision, Writing – review & editing. JL: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Applying portfolio theory to benefit endangered amphibians in coastal wetlands threatened by climate change, high uncertainty, and significant investment risk

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The challenge of selecting strategies to adapt to climate change is complicated by the presence of irreducible uncertainties regarding future conditions. Decisions regarding long-term investments in conservation actions contain significant risk of failure due to these inherent uncertainties. To address this challenge, decision makers need an arsenal of sophisticated but practical tools to help guide spatial conservation strategies. Theory asserts that managing risks can be achieved by diversifying an investment portfolio to include assets – such as stocks and bonds – that respond inversely to one another under a given set of conditions. We demonstrate an approach for formalizing the diversification of conservation assets (land parcels) and actions (restoration, species reintroductions) by using correlation structure to quantify the degree of risk for any proposed management investment. We illustrate a framework for identifying future habitat refugia by integrating species distribution modeling, scenarios of climate change and sea level rise, and impacts to critical habitat. Using the plains coqui (*Eleutherodactylus juanariveroi*), an endangered amphibian known from only three small wetland populations on Puerto Rico's coastal plains, we evaluate the distribution of potential refugia under two model parameterizations and four future sea-level rise scenarios. We then apply portfolio theory using two distinct objective functions and eight budget levels to inform investment strategies for mitigating risk and increasing species persistence probability. Models project scenario-specific declines in coastal freshwater wetlands from 2% to nearly 30% and concurrent expansions of transitional marsh and estuarine open water. Conditional on the scenario, island-wide species distribution is predicted to contract by 25% to 90%. Optimal portfolios under the first objective function – benefit maximization – emphasizes translocating frogs to existing protected areas rather than investing in the protection of new habitat. Alternatively, optimal strategies using the second objective function – a risk-benefit tradeoff framework – include significant investment to protect parcels for the purpose of reintroduction or establishing new populations. These findings suggest that leveraging existing protected areas for species persistence, while less costly, may contain excessive risk and could result in diminished conservation benefits.

Although our modeling includes numerous assumptions and simplifications, we believe this framework provides useful inference for exploring resource dynamics and developing robust adaptation strategies using an approach that is generalizable to other conservation problems which are spatial or portfolio in nature and subject to unresolvable uncertainty.

KEYWORDS

spatial conservation planning, reserve design, portfolio optimization, risk management, habitat-species modeling, climate change, assisted migration

Introduction

Worldwide, coastal freshwater wetlands are among the most sensitive of ecosystems, resulting in increasing rates of loss as a function of anthropogenic activities (e.g., development, fragmentation and pollution) and changing climate (e.g., salinization, hydrologic alteration; Yu et al., 2019). Wetland-dependent species and the broad range of ecosystem goods and socio-ecological services provided by coastal wetlands are threatened as the distribution, extent, and function of coastal wetlands are reduced in response to relatively rapid changes in sea-level, nutrification, temperature and precipitation extremes, and altered fire regimes (Bhattachan et al., 2018; Taillie et al., 2019; Yu et al., 2019; Osland et al., 2019). Loss of coastal freshwater and tidal wetlands from sea-level rise (SLR) has been observed to result in reduced aboveground biomass, primary productivity, nitrogen sequestration, and water treatment capacity (Craft et al., 2009). Human development and other sources of habitat fragmentation are expected to limit the capacity for positive climate niche tracking of habitat or habitat-dependent species (Honnay et al., 2002; Yu et al., 2019; Zhu et al., 2021). A net loss of freshwater habitat can impact populations directly and also reduces the opportunities for marsh-dependent species to detect and migrate to areas of refugia as a means for climate adaptation.

Caribbean islands comprise a small fraction (0.15%) of global land surface area, however the region supports an inordinate representation of the worlds amphibian and reptile diversity, with 3% of all amphibians and 6.3% of the world's reptiles occurring in the West Indies (Hedges, 1996). Similarly, Caribbean islands have seen a disproportionate level of anthropogenic impacts (e.g., development, forest loss, fragmentation, invasive species) (Martinuzzi et al., 2007; Collazo et al., 2018) and are expected to experience greater changes in climate extremes relative to baseline experience in temperate regions or continental landmasses with accelerated SLR, salinization of freshwater resources, erosion, extreme periods of precipitation and drying (Jennings et al., 2014; Nurse et al., 2014). Amphibians are among the most sensitive vertebrate groups to rapid environmental changes, largely the result of limited vagility, narrow distributions, and habitat specialization (Joglar et al., 2011; Case et al., 2015; Zhu et al., 2022; He et al., 2023). Puerto Rico was among the first regions to observe declining amphibian populations possibly attributed to climate change and other anthropogenic impacts (Joglar et al., 2011). To protect sensitive biodiversity and ecosystems from climate change on small tropical islands, the natural resource management community is tasked with exploring, adopting, and implementing novel conservation strategies to address proximate factors affecting amphibians and other species at appropriate planning scales.

Towards this end, we present a test-case to demonstrate a potential strategy for localized adaptation planning for species conservation in response to observed and projected global change impacts to important coastal systems. We selected an endangered and endemic amphibian, the plains coqui (*Eleutherodactylus juanariveroi*; Spanish: coqui llanero; hereafter llanero), on the island of Puerto Rico to represent a spatially discrete natural resource management issue of modest spatial scale. This species is a coastal, fresh-water wetland-obligate species with a highly restricted known distribution, currently believed to be limited to three small, isolated habitat patches on the island's northern coastal palustrine fringe (Figure 1). We believe the species was once widely distributed throughout the northern coastal plain (Collazo et al., 2023), but has been restricted to isolated marsh patches due to land-use change and altered hydrology. Llanero is the smallest bodied of Puerto Rico's 17 extant *Eleutherodactylus* species (14.7-15.8mm mean snout vent length) and is thought to occupy the smallest geographic distribution on the island. Since llanero was first identified from a single wetland in 2007 (Ríos-López and Thomas, 2007; Ríos-López et al., 2014), there have been recent discoveries of two additional isolated populations (Figure 1).

Puerto Rico's coastal wetlands have been highly modified by humans since the 1500s, mostly in the form of agriculture; widespread urbanization of the northern coast has been the dominant source of land-use change since the 1930s (Ríos-López and Thomas, 2007). Wetlands of the northern coastal zone are maintained by high aquifer discharge provided by the island's adjacent karst region. This discharge extends the hydroperiod on the coast, favoring marsh over forested wetland habitat (Lugo et al., 2001). These wetlands are characterized by emergent, seasonally flooded herbaceous non-saline wetlands dominated by ferns,

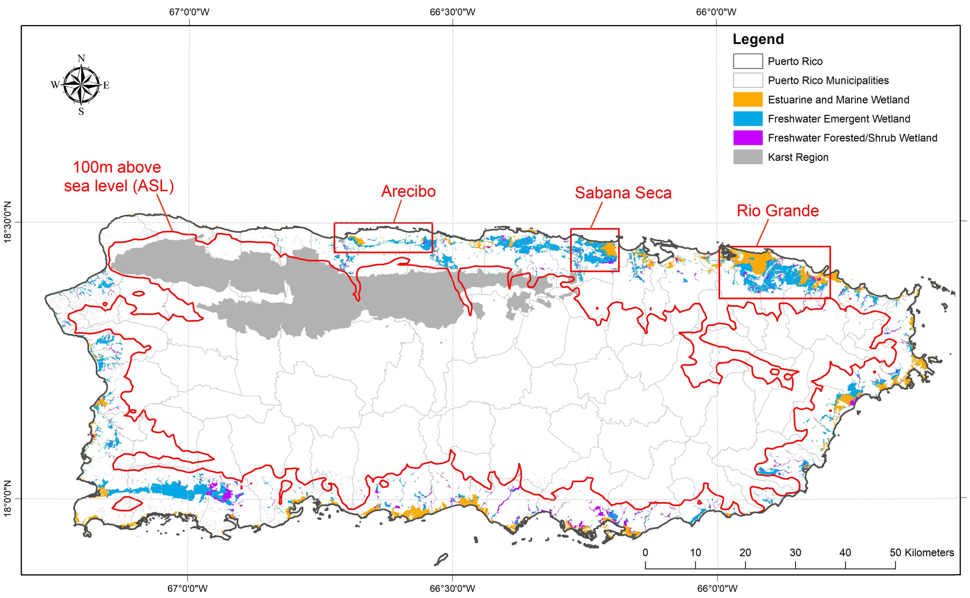

FIGURE 1
The island of Puerto Rico depicting the current distribution of coastal wetlands and the extent of the island's karst geology. Outlined in red are the arbitrary boundaries representing the three currently known populations of the plains coqui (*E. juanariveroi*, "coqui llanero"): Sabana Seca population, discovered in 2005 (Ríos-López and Thomas, 2007) with critical habitat designated in 2012 (USFWS (United States Fish and Wildlife Service), 2012); the Arecibo population, discovered in 2022 (Morales-Pérez et al., 2022); and the Rio Grande population, discovered in 2023.

flatsedges, rushes, grasses, and intermittent stands of the tree *Pterocarpus officianalis* (Ríos-López and Thomas, 2007; Yu et al., 2019). The bulltongue arrowhead (*Sagittaria lancifolia*) has been hypothesized to serve as an obligate substrate for llanero reproduction; its presence thus regulating the population dynamics and distribution of coqui llanero (Ríos-López et al., 2014). The coastal plains of Puerto Rico are particularly threatened by multiple factors. The rate of SLR recorded in northern Puerto Rico has advanced dramatically in recent years, with a 6-fold increase from 2.08 mm/year over the period 1962 to 2016 to 12.12 mm/year between 2010 and 2016 (Yu et al., 2019). Current mean elevation of coastal wetlands does not exceed 17m above mean sea-level (MSL; Ríos-López and Thomas, 2007) but most llanero localities are at less than 5m above MSL (pers. obs.). The potential of coastal marshes to naturally track SLR landward is effectively restricted by development and may be limited to river valleys and some riparian zones that have escaped development (Yu et al., 2019). In addition to urbanization, SLR, and future salinization of freshwater wetlands, other threats to the species include recreation, contamination from landfills, habitat damage from flood control, and competition or predation by invasive species (Ríos-López et al., 2014). As a result of these threats to Puerto Rico's coastal wetlands, coqui llanero was designated as endangered by the U.S. Fish and Wildlife Service in 2012 (Ríos-López et al., 2014).

Climate change has been identified as a factor that may affect the demographics, abundance, and distribution of Puerto Rico's natural resources, either directly (Jennings et al., 2014; Rivera-Burgos et al., 2021) or indirectly (e.g., through increased disease transmission; Burrowes et al., 2004; Joglar et al., 2011). The island is predicted to experience warming and drier conditions especially in the rainy season (Bowden et al., 2021). These changes will exacerbate the vulnerability of both coastal wetlands and temperature- and humidity-sensitive amphibians, including coqui llanero. In addition to protecting viable and resilient habitat within the current species distribution, an important strategy for conserving amphibians threatened by changing biotic and abiotic conditions is to secure habitat refugia (i.e., sites predicted to develop analog conditions into the future) in advance of these changes. Such sites could be protected adjacent to existing habitat, allowing for a gradual evolution of conditions (i.e., marsh migration, elevational climate tracking) at a velocity compatible with species' natural dispersal capacity. An alternative approach is to use climate model simulations to identify future analog sites wherever they may exist; protecting and, if needed, restoring these sites now will increase adaptation options for future conservation measures, such as reintroductions to sites believed to be in the species' historical range, assisted migration (i.e., translocation) to sites beyond the known indigenous range, or developing a connected network of migration corridors between existing protected areas. As of 2016, the government of Puerto Rico reported it had achieved a target of 16% of lands in various forms of conservation status (LCC Network, 2016).

We develop our test-case using multiple climate adaptation strategies to maximize the viability of a sensitive amphibian species of conservation importance. We begin by evaluating projected changes in future conditions of coastal wetlands, including SLR, altered precipitation regimes, and habitat transitions, to predict the possible impacts on the status and distribution of extant llanero populations. We consider a range of future scenarios to project the distribution of wetland refugia on the island; these become candidate sites for possible management interventions (e.g., protection, restoration, species reintroduction or assisted migration). Recognizing the uncertainty inherent in these climate and habitat scenarios, we then conduct a spatial portfolio analysis to demonstrate a well-grounded approach for managing the risk of investing in conservation actions to meet objectives for securing long-term resource persistence.

Methods

Modeling species and habitat distributions

For the purposes of this demonstrative model, we were limited in the number of parameters, level of detail, and sophistication in projecting future biotic and abiotic conditions of the island's coastal wetlands. For recent historical observations (1963-1995), we characterized monthly precipitation and minimum and maximum temperatures using data based on the Parameter-elevation Regressions on Independent Slopes Model (PRISM, Daly et al., 2003) and made use of high-resolution global climate data for other abiotic variables provided by WorldClim (1970-2000; Fick and Hijmans, 2017). Biotic variables include landcover classification from year 2000 (Kennaway and Helmer, 2007), wetland habitat classification (Federal Geographic Data Committee, 2013), and soils data from the U.S. Department of Agriculture's Natural Resources Conservation Service (NRCS; Soil Survey Staff, 2021). We used projected precipitation and temperature data for the period 2040-2060 under a higher greenhouse gas emissions scenario (RCP8.5) using dynamically downscaled climate model outputs produced for Puerto Rico at a 2km resolution (Bowden et al., 2021). The downscaled climate model projections were bias-corrected based on the PRISM using a simple delta approach (Hay et al., 2000) before using the values in any ecological models.

We developed a candidate set of niche models to estimate the species' distribution under current conditions and to characterize habitat affinities and potential abiotic determinants of the species' range based on the conditions of known localities (i.e., niche envelope). Species data for fitting distribution models consist of approximately 45 presence-only observational records with locality information from personal observations and a public database (GBIF, 2023) used to characterize environmental and abiotic conditions to which the species is currently exposed. Although there have been widespread, *ad hoc* efforts to establish the distribution of coqui llanero (Dávila Casanova, 2021), to our knowledge no systematic occupancy surveys have been performed that could be used for quantifying the detection process (MacKenzie et al., 2017) and for estimating putative species absences. To address this, we included a random sampling of background points distributed over the environmental and abiotic conditions of Puerto Rico's coastal fringe (i.e., <100m above MSL) to characterize the variability of conditions where we assume the species may be absent (i.e., "pseudo-absence" data; Phillips et al., 2009). Because of the limited number of positive species records, we were unable to evaluate an exhaustive list of covariates explaining possible habitat affinities or avoidance. Instead, we focused on a small number of reasonable, *a priori* candidate factors including habitat classification and abiotic climate variables. Biotic variables include landcover classification, the refined wetland classification, and soil type. For climate variables, we used the PRISM data to derive mean annual precipitation, mean rainfall over the driest period (Feb-Mar), means of the two highest rainfall months (May and Nov), minimum temperature of the coldest month, and mean temperature of the north coast's wettest quarter. Given the widespread conversion of wetland habitat to agriculture and urban development (Collazo et al., 2018; Yu et al., 2019), we hypothesize that low-lying, drained freshwater wetlands were likely to have supported llanero populations in the recent past and may represent additional viable habitat for llanero expansion (i.e., through migration or reintroduction) if these areas were to be restored. To evaluate this possibility, we estimate coefficient values for an alternate model specification by adding to the dataset 15 randomly assigned, hypothetical observations to those wetlands classified as drained or partially drained hydric soils (Cowardin et al., 1979; Federal Geographic Data Committee, 2013).

Using combinations of the selected covariates and their values for known llanero observation locations and background locations, we modeled the species' current environmental niche by specifying a generalized linear model (GLM), using a logistic link function to relate the response variable (probability of occurrence) to a linear combination of habitat and environmental factors at a given location. Assuming upland regions of the island, where wetland habitats are mostly absent, will not be suitable to support llanero populations, we reduced the domain of our analysis to Puerto Rico's coastal plains (<100m MSL). This area encompasses the three known populations and the majority of palustrine wetlands on the island's coastal zone. We focus on three sub-regions around each of the three known populations (Figures 1, 2) to summarize and compare current wetland conditions and distributions to those projected under various future scenarios in greater detail. We evaluated a series of modeled combinations of current environmental variables for their fit to the data, using lowest values of AIC to select a final set of covariates that best explain variation in llanero occurrence and distribution (Burnham and Anderson, 2010). For each sub-region we evaluate the proportion of area predicted to have a high probability (>0.6) of current llanero occurrence. We retain the best-fit model under current conditions when evaluating changes in species distributions conditional on future environmental projections.

To model projected changes in species distributions and potential habitat refugia, we would ideally consider multiple hydrological processes that are sensitive to changes in precipitation and rising ocean levels, including freshwater recharge, changes in the water table, hydrologic head gradient, and the fresh water-saline water interface. Such models would then inform predictions of vegetation transitions and other biotic changes, but are not currently available to explicitly model these coastal processes. Instead, we rely on available covariate data to estimate changes under future climate scenarios, including precipitation and temperature projections and habitat transitions linked to SLR scenarios, as well as some static variables such as soils and wetland data layers. For changing sea levels, we rely on an available scenario-based model of SLR which projects spatially

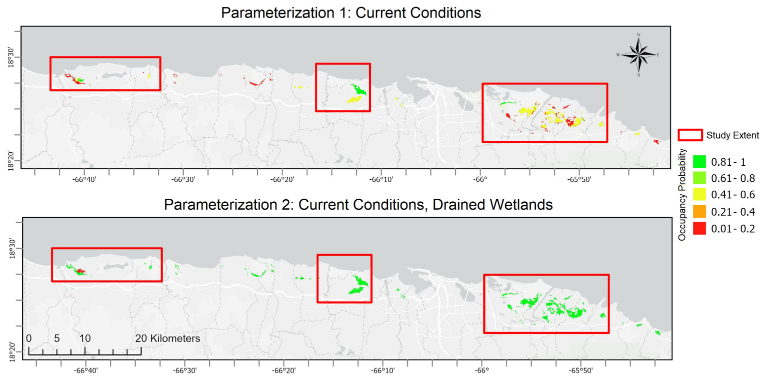

FIGURE 2
Modeled distributions of the plains coqui (*E. juanariveroi*, "coqui llanero") across Puerto Rico's north coast as a function of current select environmental conditions and under two model parameterizations. Parameterization 1 was modeled using known localities, none of which occur in drained wetlands, whereas Parameterization 2 hypothesizes drained wetlands represent valuable habitat for the species if restored. Red boxes denote the sub-regions analyzed in this study (see Figure 1 for the named designations and full spatial extent).

resolved changes in habitat cover types over a range of uncertain climate futures and sea levels, including scenarios of 0m (no change), 1m, 2m, and 3m SLR (SLAMM; Clough, 2008). Because future sea-levels were not attributed probabilistically to any given time horizon, the horizon used for climatological projections (2040-2060) represents the period for which the decision optimization is directed. Thus, the range of possible interactions between future precipitation and sea levels constitute an additional, unmodeled source of uncertainty. For each of the resulting eight scenarios – four SLR values with and without hypothetically restored wetlands – we then identified potential future refugia across the north coast with high predicted occurrence probability (>0.6) for further management consideration. All distribution modeling was performed in R (R Core Team, 2021) with the exception of reprojecting some spatial layers using ArcGIS Pro (ESRI v3.1).

Decision analysis using portfolio optimization

Significant and long-term investment is typically required for designing, implementing, or modifying a protected area network. We therefore propose the use of a quantitative portfolio optimization approach that accounts for uncertainty, spatial variability, and risk when evaluating any set of proposed investments in a conservation design (Markowitz, 1959). We evaluated the optimal allocation of resources to conserve an endangered amphibian through assisted migration, habitat restoration, and protection of future refugia under two related but distinct objectives for portfolio optimization: maximizing cumulative occurrence probability (benefit) constrained by a range of management budgets, and a two-objective problem balancing benefit maximization with the risk of investing in a conservation portfolio that performs poorly if an unexpected future unfolds. For either optimization approach, we use modern portfolio theory (MPT), a method which formalizes investment diversification as an explicit strategy to manage risk under uncertainty (Markowitz, 1959). MPT was developed in economics for addressing market uncertainty by postulating that an investment asset should not be assessed in isolation but that portfolios of assets be considered based on total expected benefits and by how each asset in the portfolio co-varies with all others as conditions (e.g., market, climate, or other) fluctuate. This approach quantifies risk by integrating a measure of asset variance over uncertainty and the correlation structure among asset pairs. Ignoring topographic, habitat, or political boundaries, we define a regular hexagonal grid (1000m resolution) across the focal domain coincident with areas below 100m MSL. We treat each grid cell as the unit of decision making (i.e., a potential asset to protect as current or future species refugia) and quantify expected benefit (EV) of the grid cell by taking the average projected occurrence probability from the distribution modeling (25m resolution) for each future scenario. We calculate the variance of each cell (var[EV]) and quantify risk by considering individual asset variance and how refugia quality covaries among all asset pairs over the range of future scenarios (Eaton et al., 2019, 2021). We model SLR as independent of future emission or warming scenarios and therefore do not assign probabilities to SLR scenarios; thus, we calculate EV, var[EV], and asset covariance as equally weighted.

For the optimization model, we consider both currently protected areas (PA; Protected Areas Conservation Action Team, 2018) and unprotected sites, aggregated to the resolution of the grid cell (i.e., a protected area is comprised of ≥1 grid cell). We identify previously drained wetlands and aggregate these as unique assets where they intersect with grid cells and further classify these as currently protected or unprotected cells. Finally, grid cells intersecting with areas of known llanero presence are classified as occupied. To reduce the dimensionality of the optimization problem, we further constrain the number of grid cells within the island's coastal zone by including only those comprising protected areas, drained wetlands, cells with known llanero occupancy, and cells with a non-zero probability of occupancy across any of the four SLR scenarios. This approach reduces the decision space from >10,000 cells (island-wide), to 3,950 cells across the coastal zone

(<100m MSL), to a final problem size of 925 grid cells included in the optimization. Because of the difficulty of assessing land values across Puerto Rico, we make simplifying assumptions regarding the costs of translocating frogs, protecting or restoring land assets, and monitoring existing or translocated populations. We assign a unit cost of 0.5 for implementing a translocation to an unoccupied cell. For each unprotected 1 km^2 cell, we ascribe a cost of 1.5 as the cost to put the asset into protected status (i.e., purchase or put into a conservation easement at a cost of 1.0) and conduct the translocation. Because these are identified as climate-analog cells (i.e., matching expected future climate at one location with the current climate at another known location; Fitzpatrick and Dunn, 2019), we assume restoration is not required. We therefore assign a cost of 0.5 to translocate frogs to cells falling within a PA, assuming there is no additional cost to conserve or restore these parcels. Because the reserve design optimization software considers the possibility of divesting from a PA to add the recovered funds to the design budget (Ghasemi Saghand et al., 2021), we modified the protected status of PA cells so they would be ignored for translocation rather than be selected for divestment. For unprotected, drained wetland sites, we assign a unit value of 2.0 to account for the cost to protect and restore these sites prior to conducting a translocation. Therefore, a cost of 1.0 is assigned to drained wetlands falling within a PA, reflecting the costs of restoration and translocation. Finally, we assume a nominal cost of 0.05 for monitoring currently occupied sites. With these specifications, our optimal spatial portfolios include decision outcomes reflecting nine possible management actions for each of the 925 grid cells evaluated – 1) disregard an unprotected cell, 2) conserve an unprotected cell and translocate frogs, 3) translocate to a currently protected cell, 4) disregard a protected cell, 5) restore and translocate to a protected drained wetland, 6) conserve, restore and translocate to an unprotected drained wetland, 7) disregard a drained wetland cell, 8) monitor a currently occupied cell, and 9) discontinue investing efforts into a currently occupied cell.

We evaluate reserve designs under two optimization frameworks and across a range of unit-cost budget scenarios. We developed a range of budget constraint scenarios, using unit-costs values of {10, 30, 50, 75, 100, 150, 200}, based on a set of trial model runs, with the highest budget scenario corresponding to the point where no changes in portfolio decisions or values were observed. The two forms of optimization included a cost-constrained maximization and a risk-benefit tradeoff analysis. The former strategy focuses on maximization of expected occurrence value conditional on budget constraints, while the latter prioritizes trading off expected return with risk minimization using a Nash bargaining solution (Nash, 1950; Eaton et al., 2019) under each budget-constrained scenario. We performed all portfolio optimizations using the SiteOpt package (Ghasemi Saghand et al., 2021) in R. SiteOpt was designed to solve large portfolio optimizations by solving a series of smaller, binary linear or quadratic optimization problems that obviate the need to compute the full Pareto-optimal frontier (Sierra-Altamiranda et al., 2020). The SiteOpt optimization model allows us to efficiently identify the best and worst values for each objective (return, cost, risk) independently, and find Nash-optimal solutions that balance bi-objective problems (e.g., cost *vs.* benefit or benefit *vs.* risk) by identifying the location on the Pareto frontier where the volume of dominated alternatives is maximized (Santín et al., 2017; Eaton et al., 2019; Sierra-Altamiranda et al., 2020; Supplementary Figure S1). For each budget scenario, we quantify the proportion of the maximum possible management return produced by the optimum,

$$PB_b = \frac{\Sigma(\psi_S * x_{i,b})}{\Sigma(\psi_S)} \quad (1)$$

where PB_b is the proportion of total benefit provided by an optimal portfolio at budget level b, ψ_S is a vector of occurrence probabilities for each grid cell (unweighted expected values across S environmental scenarios), and $\boldsymbol{x}_{i,b}$ is a vector of binary decision variables which take a value of one if grid cell i is identified for a conservation action (i.e., protection, restoration or translocation) and zero if no action is recommended for cell i under budget level b. We also evaluate the proportion of the ideal benefit for the optima under each budget level, as well as the proportion of worst-case risk or costs (i.e., nadir of the Pareto frontier) for each optima incurred at a given budget level (see Equations 5-8 in Sierra-Altamiranda et al., 2020). Evaluating the trends produced by these tradeoffs can provide insights to decision makers regarding idealized levels of funding to maximize rates of increase in management return and, alternatively, to minimize rates of loss (i.e., cost and risk). For each of the two optimization frameworks and under each level of investment, we additionally quantify the number of new parcels recommended to add to the PA network and the average value each decision category contributes to the total expected portfolio return.

Results

Current estimates of coqui llanero distribution

Applying a balance of statistical model diagnostics (e.g., minimized AIC values) and biological knowledge of the species (Porfirio et al., 2014), we used a stepwise approach to evaluate combinations of covariates to select a final model for predicting species distribution. The model with the lowest AIC included categorical variables of landcover class, soil type, and wetland category, as well as a continuous variable of average monthly rainfall during the driest period (Feb-Mar). The next best-supported model included these same variables with the exception of precipitation. Selected covariates also conform to expert understanding of drivers of llanero distribution (N. Ríos-López, pers. comm.). Based on the best-fit model and using a threshold occurrence probability > 0.6, the area occupied in Arecibo is estimated to be approximately 32 hectares (0.5% of the undeveloped habitat extent in the demarcated sub-region), 179 hectares (3.6%) in Sabana Seca, and 53 hectares (0.4%) in the Rio Grande region (Figure 2). The overall predicted distribution of llanero across the coastal wetlands of Puerto Rico is 267 hectares or 0.1% of the potentially available habitat in the region (Table 1; Figure 2). Under the same model but including hypothesized species presence in currently drained wetlands, the predicted distributions of llanero increase considerably. The overall prediction of potentially occupied area for the island's coasts increases to approximately 1930 hectares, a more than 7-fold expansion relative to the initial parameterization (Table 1; Figure 2).

Projected changes to abiotic conditions and coastal wetlands

Puerto Rico's northern coastal plains and karst region fall within the subtropical moist forest life zone (Khalyani et al., 2016). Daily average minimum temperatures are projected to increase from 1.2—1.5°C and maximum temperatures by 1.1 to 1.6°C during the period 2041-2060 under the high emissions scenario and annual precipitation is projected to decline between 9 and 23%, with model-consistent reductions in extreme, afternoon, and evening rainfall (Bowden et al., 2021).

To evaluate the range of projected changes in abiotic conditions at the scale of current llanero distribution, we compared historical to future projected mean precipitation values for our delineated coastal region. To do this we took the original downscaled output from Bowden et al. (2021) and calculated the percent differences in mean monthly precipitation at each 2km grid cell of the projection period (2040-2060) compared to the historical model simulation period (1985-2005). Then, we applied these percent differences to the PRISM data (Daly et al., 2003) over that dataset's analysis period (1963-1995) to obtain estimated changes in the absolute amount of mean precipitation. We assume that even though there is only partial overlap between the PRISM historical period and the historical climate model simulation period, the two periods are climatologically (and statistically) similar since both dataset periods represent times before the global anthropogenic signal had significantly emerged. We apply this procedure, rather than directly using the percentage precipitation change from the climate model simulations because the absolute precipitation values are required for the species distribution models. Under the RCP8.5 scenario, average monthly rainfall in our study area for the driest two months (Feb-Mar) is projected to decline 16% by the middle of the century from a current monthly average of 70 mm (Figure 3A). Precipitation during the wettest month (May), currently averaging 198 mm, is projected to decrease by 23% with the greatest declines projected to occur over the northwestern karst mountains and in the eastern cordillera (Figure 3B).

Current freshwater marsh (based on an *a priori* SLR scenario of no change) is estimated to cover approximately 16% of the coastal fringe, with the three sub-regions comprising a much higher representation of potentially suitable marsh habitat (Arecibo: 38%, Sabana Seca: 38%, Rio Grande: 33%; Table 2A). Across the three additional *a priori* SLR scenarios (1m, 2m, 3m), SLAMM output predicts substantial loss of freshwater marsh (ranging from less than 1% to 3.5%), with the highest expected losses being inland freshwater marsh and irregularly flooded marsh (losses as high as 27% and 20%, respectively, under the highest predicted SLR). Transitional marsh is projected to more than triple in area, open estuary area experiences up to a four-fold increase, and ocean beach expands more than three-fold under the 3m SLR scenario (Table 2B). Projected wetland losses are not distributed equally across the three llanero sub-regions. Regardless of the scenario, Sabana Seca is projected to experience the greatest relative loss of critical habitat, from 20% to 73%. The Rio Grande and Arecibo areas are projected to experience similar levels of loss, from 2% and 3% under a minimal SLR and 42% and 44% under highest SLR, respectively.

Projected changes in coqui llanero distribution and identification of habitat refugia

Interactions of climate change with SLR-driven habitat transitions are expected to result in significant changes to the species' distribution, with somewhat unexpected spatial variation over the modeled scenarios. Using a threshold probability of

TABLE 1 Projected area (hectares) and percent of sub-regions occupied by coqui llanero under current sea levels and for scenarios of 1-3m sea-level rise (SLR).

	Area Occupied (Ha)					Percent Area Occupied			
Model 1	0m	1m	2m	3m		0m	1m	2m	3m
AR	31.5	31.5	23.1	0.0	AR	0.5%	0.5%	0.3%	0.0%
SS	178.8	115.7	9.1	1.3	SS	3.6%	2.3%	0.2%	0.0%
RG	52.9	51.4	36.9	22.4	RG	0.4%	0.4%	0.3%	0.2%
Coast	267.0	202.4	71.9	26.1	Coast	0.1%	0.1%	0.0%	0.0%
Model 2	0m	1m	2m	3m		0m	1m	2m	3m
AR	136.3	136.3	69.3	25.4	AR	2.1%	2.1%	1.0%	0.4%
SS	346.8	282.8	156.5	120.8	SS	7.0%	5.7%	3.1%	2.3%
RG	1,159.3	1,144.1	795.1	580.5	RG	8.5%	8.4%	5.8%	4.2%
Coast	1,932.6	1,853.4	1,303.9	967.1	Coast	0.9%	0.9%	0.6%	0.5%

Model 1 estimates distribution based on habitat niche derived from observed positive localities. Model 2 includes drained wetlands as candidates for species occurrence assuming restoration of hydrologic properties. Four sub-regions are represented: Arecibo (AR), Sabana Seca (SS), Rio Grande (RG), and the island's coastal zone below 100m above sea-level (Coast).

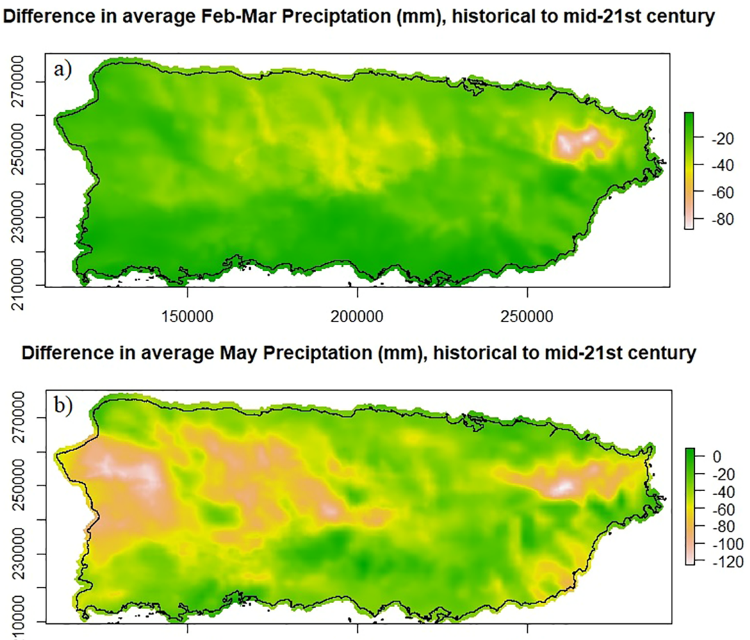

FIGURE 3
Projected declines in precipitation across Puerto Rico for **(A)** the dry season (Feb-Mar) and **(B)** the month of highest precipitation (May). Declines are visualized as differences between mean monthly historical (1963-1995) and mid-century (2050) projections.

occurrence of >0.6 to estimate area occupied, a 1m SLR scenario is projected to have no impact to llanero distribution in Arecibo but results in a 35% decline in the occupied area in Sabana Seca. Under the 2m SLR scenario, the projected loss of occupied area ranges from 95% in Sabana Seca to a 27% loss in Arecibo. A 3m SLR scenario would result in total extirpation of the population in Arecibo and a decline in occupied area of ~58% in Rio Grande. Across the three SLR scenarios, the entire coastal zone would experience average losses in llanero distribution of 25%, 73%, and 90%, respectively (Table 1; Figure 4). Predicting changes in llanero distribution under the second parameterization (which models occupancy assuming drained wetlands are currently occupied) resulted in similar patterns of reductions in species distribution with increasing SLR, although with overall greater extents of area occupied and larger proportional losses under rising seas (Table 1). Despite the disparities in projected habitat-area loss over the three population sub-regions, shifts in future habitat refugia follow a similar pattern, with refugia projected to shift landward over SLR scenarios, suggesting saltwater intrusion or habitat transition may be stronger drivers of population dynamics relative to changes in rainfall, temperature, or other factors. The consequences of these dynamics of near-coast habitat loss, and potential inland habitat gains, is a shift away from areas of known occupancy, particularly in Arecibo marshes (Figure 4). Under the second parameterization (drained wetlands modeled as potential habitat), llanero is predicted to be more widely distributed relative to the original parameterization (Table 1), including scattered distributions beyond the northern coastal plains to eastern wetlands (Figure 5). Although the area of occupancy declines with increasing SLR, at an occupancy probability threshold >0.6, the predicted distribution increases when using this more permissive niche parameterization relative to the first parameterization. This suggests the potential opportunity for expanding freshwater habitats (e.g., transitional marsh; Table 2A) to act as refugia for llanero as ocean levels rise (Figure 5).

Portfolio optimization for a risk-managed adaptation to climate change

The covariance structure of expected parcel benefits across climate scenarios revealed that the majority (95.2%) of grid-cell pairs are either uncorrelated or negatively correlated with changes in SLR (i.e., < 4.8% of cell pairs co-vary positively across scenarios). A neutral (uncorrelated) or negative (one parcel improves while the other declines under a given scenario) relationship between pairs allows for managing risk through diversification of a reserve portfolio with sites that bet-hedge over the full range of climate uncertainty. This contrasts with a strategy of selecting those parcels which are individually expected to provide the highest benefits (i.e., averaged over scenarios). Our cost-constrained optimization approach did not include this risk-mitigation but produced results comparable to the risk-return framework (Table 3). This outcome may be due in part to the small percentage (< 1%) of negatively correlated site pairs contributing to the neutral or negative relationships among parcels, suggesting that bet-hedging opportunities for coastal sites may be limited and, thus, managing risk may not play as large a role in protected area design for coastal Puerto Rico as might be expected. Under this first approach, our evaluation of SLR scenarios across the coastal zone offers evidence

TABLE 2A Distribution of landcover classes under current conditions, in hectares, for the sub-regions designated in this study.

Habitat Class	Arecibo	Sabana Seca	Rio Grande	Coastal
Developed Dry Land	779	938	3,707	49,244
Undeveloped Dry Land	3,879	2,743	6,951	175,848
Nontidal Swamp	946	427	1,233	30,259
Inland Fresh Marsh	1,558	1,157	2,447	2,604
Transitional Marsh	214	332	2,318	1,123
Ocean Beach	37	10	22	322
Estuarine Open Water	1	–	0	1
Tidal Creek	2	–	30	27
Open Ocean	4,100	2,218	5,384	2,739
Irregularly Flooded Marsh	21	291	915	167
Total land area	6,656	4,959	13,916	210,351
Total fresh marsh	2,524	1,875	4,595	33,029
Proportion Fresh marsh	0.379	0.378	0.330	0.157

For comparison with future changes, landcover is based on the SLAMM model (Clough, 2008). Total land area calculation excludes open ocean.

TABLE 2B Distribution of projected future landcover classes, in hectares, for Puerto Rico's coastal zone (below 100m above sea-level) as designated in this study.

Habitat Class	1m	2m	3m	Percent Difference from Current		
				1m	2m	3m
Developed Dry Land	49,210	49,048	47,987	-0.1%	-0.4%	-2.6%
Undeveloped Dry Land	175,754	175,376	174,042	-0.1%	-0.3%	-1.0%
Nontidal Swamp	30,210	30,146	29,847	-0.2%	-0.4%	-1.4%
Inland Fresh Marsh	2,546	2,270	1,902	-2.2%	-12.8%	-26.9%
Transitional Marsh	1,215	1,880	3,934	8.2%	67.4%	250.3%
Saltmarsh	10	55	351	–	–	–
Tidal Flat	3	20	50	–	–	–
Ocean Beach	337	485	1,161	4.6%	50.7%	260.5%
Estuarine Open Water	2	2	5	20.0%	85.0%	305.0%
Tidal Creek	27	27	27	0.0%	0.0%	0.0%
Open Ocean	2,742	2,753	2,783	0.1%	0.5%	1.6%
Irregularly Flooded Marsh	167	161	133	-0.1%	-3.8%	-20.2%
Total land area	210,272	210,422	211,453			
Total fresh marsh	32,923	32,577	31,883	-0.3%	-1.4%	-3.5%
Proportion Fresh marsh	0.157	0.155	0.151	0.0%	-0.2%	-0.6%

Percent changes from current conditions under 1-3m SLR are provided in the three rightmost columns. Landcover changes are based on the SLAMM model (Clough, 2008). Total land area calculation excludes open ocean.

that the location of potential refugia sites may vary spatially as a function of future climate outcomes (Figure 5). As budgets increase, a cost-constrained maximization suggests an increased focus of translocations to existing protected areas, with greater emphasis in the northeast region of the island (e.g., Rio Grande) with some new sites added to conserve wetlands near Sabana Seca and Rio Grande at very high budget levels, relative to the north-western population (Figure 6). Drained wetlands are not identified for protection or restoration under this optimization, except for one protected site under the highest budget scenario. Using this framework,

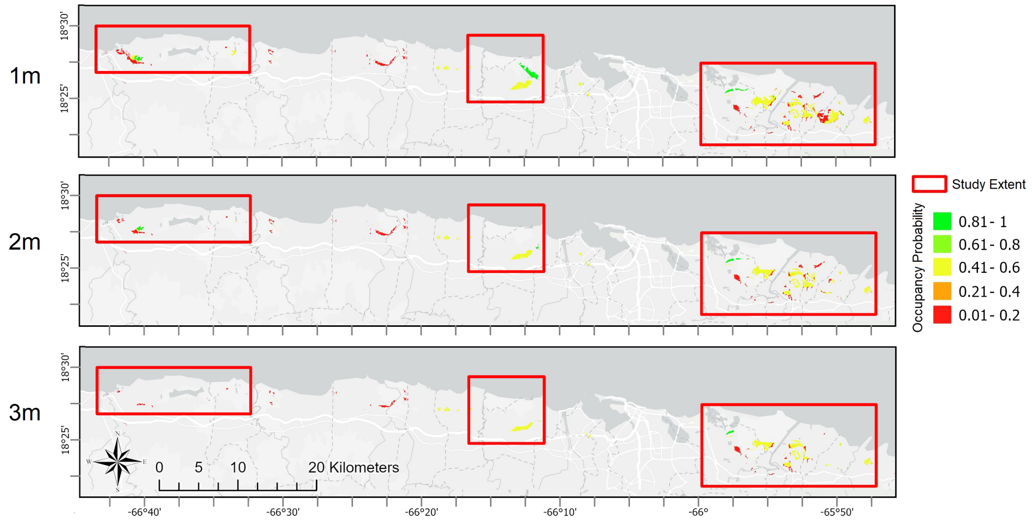

FIGURE 4
Modeled probabilities of future plains coqui (*E. juanariveroi*, "coqui llanero") distribution across Puerto Rico's northern coast, and at three sub-regions included in this study (see Figure 1). Rows represent future uncertainty in sea-levels, with scenarios of 1m, 2m, and 3m of sea-level rise (SLR).

translocating to existing PAs contributes an average of nearly 80% of the total expected conservation benefit, while adding new parcels to the reserve design contributes only 14% of the expected benefit. Continued investment for monitoring existing populations adds an average of 6% to the conservation outcome (Table 3).

We repeated budget-scenario optimizations using a Nash bargaining solution to balance expected benefits with the risks of investing in lands that may lose their conservation value conditional on climate futures (Figure 7). Surprisingly, average returns were higher across budget scenarios under the Nash approach than with the benefit-maximization framework (48.2 versus 35.9, respectively; Table 3). Relative to the previous analysis, the Nash solutions rely more heavily on conserving unprotected cells for translocating frogs and are less dependent on existing protected areas, with an average of nearly 62% of conservation benefit stemming from the protection of new land and only 33% from utilizing current PAs for species management (Table 3). Investment in the protection and restoration of a few additional drained wetlands near Arecibo and Rio Grande adds to the predicted conservation outcome, but only under a moderate budget scenario (100 cost-units; Figure 7).

FIGURE 5
Modeled probabilities of future plains coqui (*E. juanariveroi*, "coqui llanero") distribution across the northern and eastern coastal zone included in this study (see Figure 1 for the named designations) under the alternative parameterization in which predicted species distribution is modeled assuming drained wetlands represent viable habitat. Rows represent future uncertainty in sea-levels, with scenarios of 1m, 2m, and 3m of sea-level rise (SLR).

TABLE 3 Results produced for reserve design optimization under two analytical frameworks: maximization of species benefits under cost constraints and a risk-benefit optimization based on a Nash bargaining solution.

Constrained Benefit Maximization											Value Contribution								
Budget Constraint		Return	Max Return	Δ Return	% of total	Spent	Worst Cost	Δ Cost	% of Worst	Parcels Added	Ignore non-PA	Add to PA	Trans-locate to PA	Ignore PA	Restore PA drained wtlnd	Protect & restore drained wtlnd	Ignore drained wetland	Maintain and monitor	Discontinue investment
10		8.4	17.2	8.8	0.1	3.7	9.7	6.0	0.4	0	73.4	0	6.4	29.6	0	0	5.8	2.0	1.8
30		20.0	37.1	17.1	0.2	12.2	29.7	17.5	0.4	0	73.4	0	18.0	17.9	0	0	5.8	2.0	1.8
50		28.7	48.3	19.6	0.3	20.7	49.7	29.0	0.4	0	73.4	0	26.7	9.3	0	0	5.8	2.0	1.8
75		35.6	60.8	25.2	0.3	27.7	74.7	47.0	0.4	0	73.4	0	33.6	2.4	0	0	5.8	2.0	1.8
100		40.7	73.2	32.4	0.4	35.2	99.7	64.5	0.4	3	70.4	2.9	35.8	0.1	0	0	5.8	2.0	1.8
125		43.0	84.2	41.2	0.4	39.2	124.7	85.5	0.3	5	68.7	4.7	35.8	0.1	0	0	5.8	2.5	1.3
150		49.0	93.0	43.9	0.4	51.2	149.7	98.5	0.3	13	62.7	10.7	35.8	0.1	0	0	5.8	2.5	1.3
200		61.5	109.5	47.9	0.6	76.2	199.7	123.5	0.4	29	50.7	22.7	35.8	0.1	0.5	0	5.3	2.5	1.3
Mean		**35.9**	**65.4**	**29.5**	**33%**	**33.2**	**92.2**	**58.9**	**0.4**	**6.3**	**190%**	**14%**	**79%**	**21%**	**0.2%**	**0.0%**	**16%**	**6%**	**5%**
Risk-Benefit (Nash) Optimization											Value Contribution								
Budget Constraint	Spent	Return	Max Return	Δ Return	% of total	Risk	Worst Risk	Δ Risk	% of Worst	Parcels Added	Ignore non-PA	Add to PA	Translocate to PA	Ignore PA	Restore PA drained wtlnd	Protect & restore drained wtlnd	Ignore drained wetland	Maintain and monitor	Discontinue investment
10	9.6	12.7	17.2	4.5	0.1	2.7	22.3	19.6	0.1	2	71.4	2.0	8.8	27.2	0	0	5.8	2.0	1.9
30	29.7	30.2	37.1	6.8	0.3	65.7	520.3	454.6	0.1	10	64.9	8.5	19.3	16.7	0	0	5.8	2.5	1.3
50	49.7	39.3	48.3	9.0	0.4	113.1	673.1	559.9	0.2	24	54.4	18.9	17.9	18.1	0	0	5.8	2.5	1.3
75	73.1	49.0	60.8	11.8	0.4	209.0	940.0	731.0	0.2	39	44.7	28.6	18.2	17.8	0	0	5.8	2.3	1.6
100	91.1	52.3	73.2	20.8	0.5	297.6	1194.4	896.9	0.2	50	37.7	35.7	13.2	22.8	0.5	1.0	4.3	2.0	1.9
125	102.2	58.3	84.2	25.9	0.5	341.3	1651.5	1310.3	0.2	62	29.7	43.6	12.2	23.8	0	0	5.8	2.5	1.3
150	116.1	67.5	93.0	25.5	0.6	482.2	2189.6	1707.4	0.2	68	25.6	47.7	17.5	18.4	0	0	5.8	2.3	1.6
200	133.2	76.2	109.5	33.3	0.7	747.4	3892.4	3145.1	0.2	77	20.8	52.6	20.8	15.2	0	0	5.8	2.8	1.0
Mean	**75.6**	**48.2**	**65.4**	**17.2**	**44%**	**282.4**	**1385.5**	**1103.1**	**0.19**	**41.50**	**90.6%**	**62%**	**33%**	**42%**	**0.1%**	**0.3%**	**12%**	**5%**	**3%**

Bold values in bottom rows are mean quantities calculated for each column, using the units specific to the column. The means of Value Contributions columns (representing the nine possible parcel decisions) are provided as percentages of total value, with the highlighted columns summing to 100% and the sum of values for individual budget scenarios equaling the benefits provided in the column "Return" (column 3).

Recommended additions to the reserve design are again concentrated in the northcentral and northeast, with a few unprotected and currently protected cells identified for translocation along the eastern coast (Figure 7).

Although the proportion of total potential benefits increases monotonically with available budget for both the Nash solutions and the benefit-maximization optimizations, the risk-benefit framework of the Nash approach returns a greater proportion of the total available conservation benefit at each budget level relative to a benefit-maximization framework (Figure 8). This outcome suggests that overall conservation benefits may not have to be sacrificed by actively managing for risk – i.e., trading-off parcels with high expected benefit for those with lower associated risk, as theory predicts for diversified portfolios. Relatedly, the proportions of realized relative to maximum possible gains at each budget level were also systematically higher for the Nash solution, although there was no overall trend across the range of budgets under either framework (Figure 9A). However, higher proportional benefits were achieved at lower budgets (i.e., <100 cost units) in both cases. Evaluating complementary optimization outcomes of loss rates (i.e., the proportions of worst possible risks and costs incurred under each framework, respectively) reveals the Nash risk-benefit

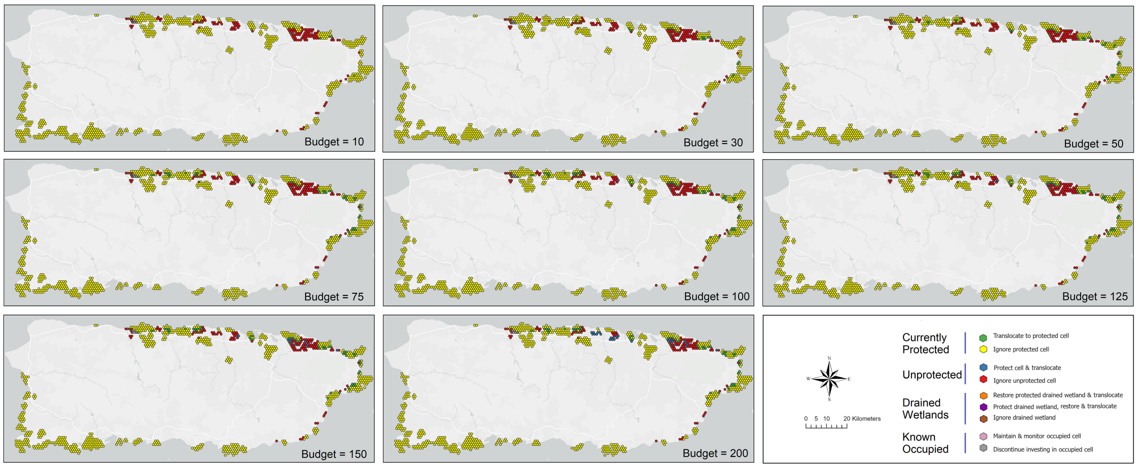

FIGURE 6
Reserve design results for coastal Puerto Rico to maximize the cumulative probability of occurrence of the plains coqui (*E. juanariveroi*, "coqui llanero") based on modeled habitat changes and projected species distributions over eight future scenarios. Optimization outcomes are constrained under eight budget levels and include nine possible management decisions, conditional on the protected-area status of a parcel and whether a parcel falls within an historical (drained) wetland.

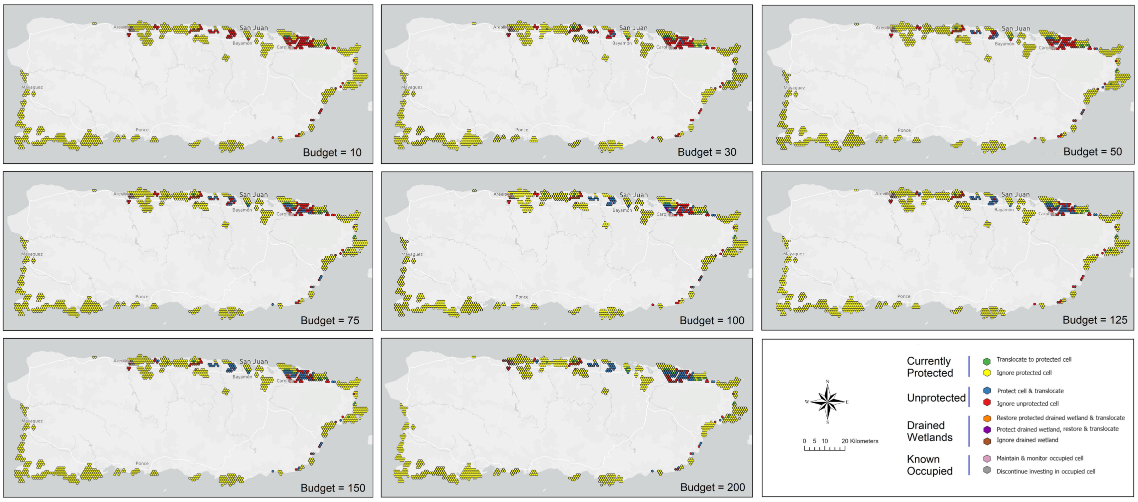

FIGURE 7
Reserve design results for coastal Puerto Rico to balance the cumulative probability of occurrence of the plains coqui (*E. juanariveroi*, "coqui llanero") and the level of risk represented by the spatial configuration and correlation structure of parcels included in a portfolio. The optimization used a Nash bargaining solution (Nash, 1950; Eaton et al., 2019) and is based on modeled habitat changes and projected species distributions over eight future scenarios. Optimization outcomes are constrained under eight budget levels and include nine possible management decisions, conditional on the protected-area status of a parcel and whether a parcel falls within an historical (drained) wetland.

framework sustained a low and relatively consistent proportion of potential risk for each budget scenario (mean of 19%; Figure 9B). In contrast, the proportion of expended costs relative to the potential was substantially greater under a benefit-maximization approach, with a mean outlay of 37% of cost potential (Figure 9B and Table 3). Note that this is a relative comparison between different framework objectives and the trends in Figure 9B represent distinct scales.

Discussion

Hedging bets as a core climate adaptation strategy

Climate change can cause direct disruptions to species persistence through physiological effects as the planet warms (Calosi et al., 2008), or via indirect effects to species' habitats or ecosystem interactions. When the conservation goal is to enhance the persistence of valued resources across a landscape in the face of uncertain future environmental change, some form of bet-hedging will be an important part of any climate adaptation strategy. When there is a spatial component to a climate adaptation problem, as is the case with designing reserve networks when future conditions are uncertain, decision makers can manage risk by leveraging the spatial correlation structure that exists among the universe of potential design elements. Theory and empirical evidence suggest that portfolios designed to maximize total expected benefits typically contain higher risk, because returns are generally calculated under "average" conditions, leading to much lower benefits if an extreme future manifests. A portfolio focused on reducing risk rather than maximization can use spatial correlation to guide a strategy of diversification which often results in lower expected returns but is more robust to any projected climate future (Eaton et al., 2019). Encouragingly, inference from our Nash optimization reveal that a risk-benefit tradeoff approach can actually produce higher absolute and percentage returns (i.e., relative to the maximum possible) than a budget-constrained maximization framework. A risk-benefit tradeoff approach was also found to result in a lower percentage of total risk relative to percent spending losses under the maximization optimization. The favorable performance of the Nash optimization may in part be due to the small percentage of negatively correlated parcel pairs available for selection, inferring that design consideration may be somewhat limited in terms of benefits to risk-reduction. Higher absolute returns, higher percentage of total possible returns, and relatively low levels of risk exposure convey the potential benefits of a balanced risk-management approach to portfolio designs for species conservation and spatial protected-area planning.

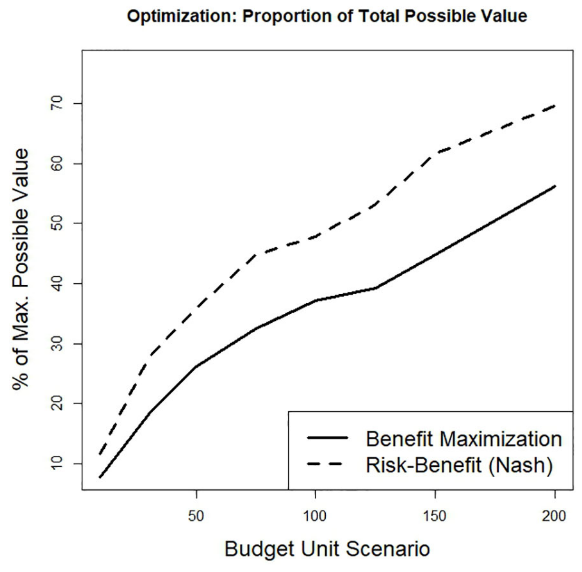

FIGURE 8
The percentage of total unconstrained available benefits (i.e., cumulative probability of occurrence) achieved under each of eight budget levels for two spatial design optimization approaches (cost-constrained maximization and balanced risk-return optimization).

Both current protected areas and the potential of drained wetlands contributed to a conservation design to increase the persistence of coqui llanero. Recommendations to protect and restore drained wetland were inevitably influenced by the second model parameterization (i.e., drained wetlands being viable llanero habitat). Cost considerations may also minimize attention given to restoring drained wetlands, with limited numbers of parcels being recommended for conservation as budgets increase (Figures 6, 7). If restoring historical wetlands is found to benefit the species, decisions to restore this habitat will likely be more important than our preliminary findings suggest. The existing PA network protects only 14% of the current predicted distribution of llanero, and conserves only 3% of the extant wetlands found along Puerto Rico's northern coast. The value of the current PA network to future conservation of llanero may still be beneficial relative to this small percent coverage, however, with 79% and 33% of the total expected benefits attributed to PAs under the constrained-maximization and risk-benefit frameworks, respectively. Importantly, cost considerations were more pronounced under the benefit-maximization framework, with an average of only 6.25 unprotected cells identified for adding to the reserve network. Under the risk management Nash approach, adding an average of 41.5 cells to the PA was assessed as optimal, even though conserving these parcels added twice the cost relative to translocating frogs to currently protected cells (Table 3). These results highlight concerns that reliance on the current protected-area network for conserving coastal species may include substantial risk. Although it was not an explicit feature of our optimization, an additional benefit of the Nash optimization results includes increased connectivity among several protected areas in the northeast (Figure 7), as well as expanding potentially valuable refugia near Sabana Seca which may support natural migration of the extant llanero population in this region.

Model limitations

Although we applied the current state of knowledge regarding factors affecting llanero distribution, including all known species localities and available data on historical and future biotic (vegetation, soils, wetlands) and abiotic (precipitation,

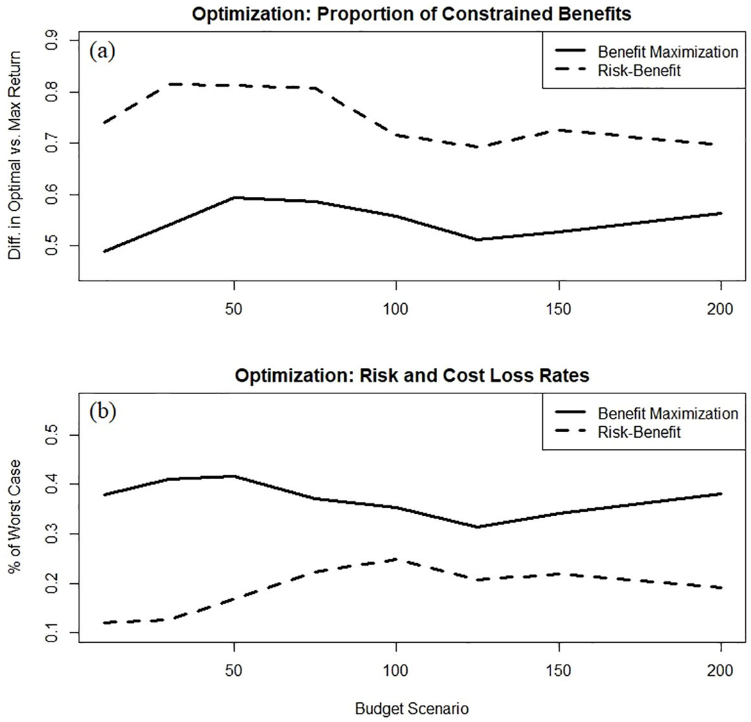

FIGURE 9
The gap between achieved conservation benefit at each budget level and the idealized benefit available for that budget for the two optimization approaches **(A)**, and the proportions of worst possible risks and costs incurred at each given budget level for the two optimization frameworks (i.e., representing the ability of each framework to minimize cost or risk losses) **(B)**. Note that in **(B)**, lower values represent better performance, and that the results from the two optimization models illustrate different metrics and are therefore not directly comparable.

temperature) conditions in coastal Puerto Rico, we simplified several aspects of our projection, species, and decision models. Simplifications affected our modeling of projected changes in habitat conditions, subsequent llanero distribution, and of the optimization of spatial conservation portfolios. Due to data limitations, we did not include coastal and karst hydrology or estimates of water-balance in projecting vegetation dynamics. Temperature-mediated evapotranspiration, declining freshwater input causing reduced hydrologic head pressure, and SLR are all expected to lead to advancing saltwater intrusion and the conversion of fresh marsh habitat to other cover types. For the decision modeling, we standardized parcel size to 1 km^2 grid cells as well as the costs to purchase, restore, translocate, or monitor. We also simplified the options available for each parcel to nine management alternatives based on expected benefits and current protection status. The implementation of one of these options, adding to a protected-area design, may not be realistic to consider for the conservation of a single species, but this practice has precedent under the “umbrella species” concept (Poiani et al., 2001; Runge et al., 2019). There will be important complexity (e.g., contextual details of translocating endangered species) to consider, in addition to other decision options available to managers (e.g., fee simple purchase versus funding conservation easements, various levels of restoration, etc.). Connectivity between cells receiving conservation action was not explicitly modeled, which could have refined the resulting portfolios and improved management benefits (Udell et al., 2018). Finally, we did not conduct an exhaustive evaluation of the sensitivity of our assumptions by simulating species distribution, habitat transition, or optimization outcomes under variations in parameter values. Our decision framework is presented as robust strategy for making long-term resource investments under substantial uncertainty, but before translocation or land-conservation decisions are implemented we advise a more thorough analysis is conducted to test the assumptions we describe. These limitations constrain the practical use of our results, but we believe the decision framework outlined here will be helpful in exploring general patterns of change, of uncertain futures, and two distinct approaches for generating optimal strategies in response.

Because of their restricted distribution and a lack of systematic survey (i.e., detection/non-detection) data, it is unsurprising that our llanero occurrence models fit a relatively few environmental variables, including landcover type, wetland categorization, soil class, and average precipitation during the driest months. Projected changes in these covariables over a range of possible climate futures resulted in substantial variation in the expected distribution of viable llanero habitat. Freshwater marshes on the island’s coastal zone are anticipated to decline under all climate scenarios, with inland freshwater marsh declining 27%, flooded marsh contracting by 20%, and non-tidal swamp experiencing a 1.5% reduction under the highest SLR scenario. Saltmarsh, transitional marsh, and tidal flats are all predicted to increase as

SLR progresses. Habitat transition and loss will not be experienced equally across the llanero distribution, with western and central populations projected to decline to near local extirpation under the highest SLR scenario while eastern populations could see reductions of less than 60% under one model. Overall losses in distribution are projected at between 50% and 90% for the northern coastal region. When modeling these habitat responses, we treated the four SLR scenarios as equally likely which could have attributed greater weight to extreme futures and biased high the expected habitat losses. Although a 3-m SLR scenario may appear extreme, updated long-term mean sea level projections for the U.S. include a range of 0.8 to 3.9m for the modeled emission scenarios by 2150 (Sweet et al., 2022). Regardless of timing or magnitude, sea-level rise and other climate-change drivers are anticipated to shift potential habitat refugia increasingly landward.

Conclusions

Although coqui llanero may be locally abundant, this tiny coastal species with limited migration ability is currently known from only three small populations in sensitive lowland marshlands, putting the global distribution of this amphibian at critical risk of extinction. Before considering localized management responses such as restoration or conservation of individual land parcels, or translocation of individuals to a “highly likely” refugia, evaluation of a more comprehensive portfolio strategy may help decision makers mitigate the risks of investing in costly, long-term activities when facing large climate uncertainty. Investing in multiple translocation sites and possibly a portfolio of land parcels is unavoidably much costlier than acting on individual protection options, but the portfolio does not have to be implemented all at once, nor by a single decision maker. Opportunities to conserve individual parcels as they become available do not have to be ignored, and optimization methods exist to advance the process we detail here by identifying an optimal sequence of parcels to conserve in an identified portfolio design (e.g., Moilanen and Cabeza, 2007; Golovin et al., 2011; Bonneau et al., 2018). An explicit and deliberative process of collaborative knowledge generation, adaptation planning, decision making, and resource sharing is one means (Johnson et al., 2020) to begin to assemble an island-wide reserve network to conserve a suite of valued species, habitats, and ecosystem processes.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://www.gbif.org/.

Author contributions

ME: Conceptualization, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. AT: Conceptualization, Formal analysis, Methodology, Writing – review & editing. JC: Conceptualization, Formal analysis, Methodology, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1444626/full#supplementary-material

SUPPLEMENTARY FIGURE 1

Properties of the Nash Bargaining Solution (Nash, 1950). With competing objectives to maximize Reward and minimize Risk, the Pareto efficient frontier (thick line) is identified and defines the solution space of dominated alternatives (light and hatched grey). The point where both objectives are maximized (U) is unobtainable. Solutions D_1 and D_2 are where Reward and Risk, respectively, are optimized at the expense of the other objective. The Nash solution optimizes the point on each axis (O_1* and O_2*, identifying N* on the efficient frontier) that maximizes the products of line segments s_1 and s_2 (i.e., the furthest combined distance from both D_1 and D_2), thereby maximizing the volume of dominated solutions (hatched grey). See Santín et al., 2017 and Eaton et al., 2019 (Appendix S1: Section S4) for equations and additional details.

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Habitat management decisions for conservation: a conceptual framework

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The focus of this selection of papers is the linkage of habitat and population dynamics for the purpose of conservation. We thus provide a general framework for making conservation decisions, emphasizing how knowledge of habitat–population linkages fits into this framework. We begin by describing structured decision-making (SDM) as a general approach to making conservation decisions. SDM requires the development of the following elements: objectives, actions, model(s), monitoring, and decision algorithm. We then describe adaptive resource management (ARM), a specific type of SDM developed for recurrent decisions characterized by potentially resolvable uncertainty. Many different classes of actions can be used to influence animal population dynamics, and modification of habitat is one class of action that is frequently used. Habitat management requires models for predicting responses of the managed system to management actions, and these models are based on our knowledge of habitat–population linkages. Frequently, these models are decomposed into two submodels: one used to predict habitat changes expected to result from management actions and another used to predict population responses to habitat changes. This latter modeling focuses generally on the influence of habitat change on vital rates governing the dynamics of population state variables (variables such as population size or density that describe the status or health of a population). Specific recommendations depend on 1) the vital rates and state variable(s) being considered, 2) the relative spatial scales of animal movement and habitat measurement, and 3) the relative temporal scales of habitat change and vital rate estimation. Finally, we present an example of an ARM program for habitat management, highlighting the role of habitat-linked population modeling in this effort.

KEYWORDS

adaptive resource management, conservation management, decision science, habitat management, population modelling, structured decision making

Introduction

Conservation of wildlife populations requires taking actions intended to meet specified objectives. One specific class of action widely used to influence wildlife populations is habitat management. Specifically, habitat quality influences populations by influencing the vital rates that determine population dynamics. Vital rates that define the dynamics of single populations are rates of survival, recruitment, immigration, and emigration. For metapopulations, the rates of local extinction and colonization are the vital rates often used to describe dynamics. Here, we describe structured decision-making (SDM) as a general approach to selecting management actions. We then describe adaptive resource management (ARM), a subset of SDM developed for recurrent decision processes that are characterized by uncertainty. Many habitat management programs are candidates for the use of ARM.

One element of SDM and ARM processes is one or more models that can be used to predict the consequences of different management actions. In the case of habitat management, such modeling frequently includes two sequential submodels: one concerning the influence of management actions on habitat and the other concerning the influence of habitat changes on wildlife population dynamics. This latter submodel is the focal topic for this collection of papers.

Our aim in this paper is to show how models linking habitat to wildlife population dynamics fit into larger conservation programs. We first describe SDM, which provides a general framework for all decisions in conservation. We then describe ARM as a special case of SDM developed for recurrent decision processes that are characterized by uncertainty. These descriptions of SDM and ARM are intentionally general, as we seek to emphasize their applicability to a wide range of decision problems.

Manipulating habitat is one class of management action used in conservation decision problems and is the focus of this set of papers. Habitat management using SDM or ARM requires models to predict the effects of these actions on system responses and "returns" (benefits, as defined by objectives). These predictions are used to make smart, even optimal, decisions within SDM and ARM programs. We thus provide a conceptual framework for using models linking habitat management to wildlife population dynamics in conservation decision processes. We provide some general observations about developing such models and using them to learn, and we describe an example of an ARM process of habitat management, highlighting the role of models in this process.

Structured decision-making

Selecting a management action represents a decision, and structured decision-making (see Martin et al., 2009; Gregory et al., 2012; Hemming et al., 2021) provides a means of making logical and transparent decisions. SDM breaks a decision process into key elements, focusing on each element separately, and then combining them to make a decision.

The SDM process should begin with an effort to define and frame the decision problem (Runge et al., 2020; Hemming et al., 2021). Problem definition identifies the issue that the decision process is intended to resolve. Framing requires identifying the decision-maker, the geographic and temporal scales of the problem, relevant laws and regulatory constraints, likely stakeholders, and key uncertainties. Attention to problem definition and framing prevents unnecessary expenditure of time and effort on vaguely defined problems.

The major elements of SDM are objectives, potential actions, model(s) of system response to actions, a monitoring program, and a decision algorithm. Objectives are simply statements of what the decision-maker and relevant stakeholders would like to achieve. Allocating adequate time and effort to the development of objectives is essential, as objectives drive the entire process, strongly influencing all of the other elements of the SDM process. Objectives may appear to be obvious, yet it is surprising how frequently like-minded stakeholders differ in their ideas about what they would like to achieve. Failure to explicitly define objectives is a common reason for the breakdown of decision processes.

Potential actions represent the set of management alternatives to be considered. The decision process is designed to select one of the potential actions for implementation, and this selection represents the decision. In some problems, the set of potential actions is clear, but this is not always the case. As with all other SDM elements, the development of potential actions should be guided by the objectives.

Models are abstractions of the managed system designed to provide specific predictions used to help the decision-maker select the best action with respect to objectives. The abstractions are frequently mathematical although this is not necessary. Indeed, models may be encoded in a computer program, the mind of the manager, or on a sheet of paper. Models useful for decision-making must make predictions about how the system responds to the different management actions. For each action in the set, the model must predict the returns and, for recurrent decisions, the subsequent state of the system. Some managers view models as interesting to academics, but not useful for people who make real-world decisions. However, if there is no way to predict the consequences of management actions, then there is no basis for selecting one option over another. Management requires predictions, so models are not optional for informed management.

Monitoring programs provide information that serves multiple needs for SDM. An estimate of a system state (e.g., abundance for single-population management) is needed for making state-dependent decisions. For example, if the population size is too small relative to our objectives, we would likely select a very different action than if the population size is too large. Monitoring also permits the manager to gauge the success of the management action. Monitoring data are frequently used to develop and improve the models required for management. In the case of recurrent decisions (see below), monitoring data can be used to learn about system responses to management.

A decision algorithm requires input from all of the other elements of the SDM process and combines these to determine which action is predicted to be best, based on expected returns. In some cases, determination of the best action to take is straightforward, but when this is not the case, optimization algorithms can be used (e.g., Puterman, 1994; Williams et al., 2002).

SDM provides a very general approach to decision-making. SDM can be used for one-time decisions (e.g., conservation land acquisition), as well as recurrent decisions, and it can be used for problems regardless of whether they are characterized by uncertainty. A key point with respect to the topic of this paper is that SDM requires models in order to predict the consequences of management actions.

Adaptive resource management

Recurrent decision processes

Recurrent decisions are made periodically, usually for the same system (Figure 1). At each decision point in Figure 1, an "action" is selected and imposed on the system. "State" refers to the general condition of the system, often assessed by the values of one or more state variables (e.g., population size, habitat type, species richness). The action generates two responses: 1) it produces returns, and 2) it drives the system to a new state (Figure 1). "Returns" are benefits, as defined by the objectives. For example, in harvest management, returns are usually defined in terms of the number of animals harvested (e.g., Johnson et al., 1997). In many other types of conservation problems, the objectives are defined in terms of the state variables that characterize the resource system. For example, returns associated with a conservation action might include change in population size (e.g., Eaton et al., 2021) or change in the probability of a population going extinct.

Recurrent decision processes impose additional complexity for decision algorithms because current decisions affect system dynamics and thus future decisions. For example, we cannot just maximize returns for the immediate time step. Instead, we must also consider the predicted state for the next time step, as objectives are typically based on the entire time horizon of the process. Recurrent decisions also admit the possibility of learning as management proceeds. Adaptive resource management is a subset of SDM developed for making recurrent decisions in the face of uncertainty about the effects of different management actions. ARM incorporates a scientific step (the comparison of observations against model-based predictions for the purpose of learning) within the larger decision process in order to reduce uncertainty and learn (Walters, 1986; Williams et al., 2007). Here, we revisit the elements of SDM from the perspective of a recurrent decision process and ARM.

ARM elements

As with SDM, objectives retain their primacy in ARM and all the other decision process elements derive from them. Objectives for recurrent decisions typically include the accrual of benefits and costs over time. Often, this is quantified by simply summing returns over the time horizon of the process. Time may also be incorporated by defining the objective in terms of a specific time interval, for example, when our objective is to minimize the probability of a local population going extinct over a specified time horizon (e.g., the next 50 years), as computed via population viability analysis (Beissinger and McCullough, 2002).

The set of potential actions for recurrent decisions may remain fixed for the entire process or it may evolve. Recurrent decisions admit the possibility of modifying the set of actions, either adapting them to a changing system or else considering new alternatives (see *Double-loop learning*).

The role of models in decision processes is to project the consequences of management actions. Models for one-time decisions may only need to predict immediate returns, but

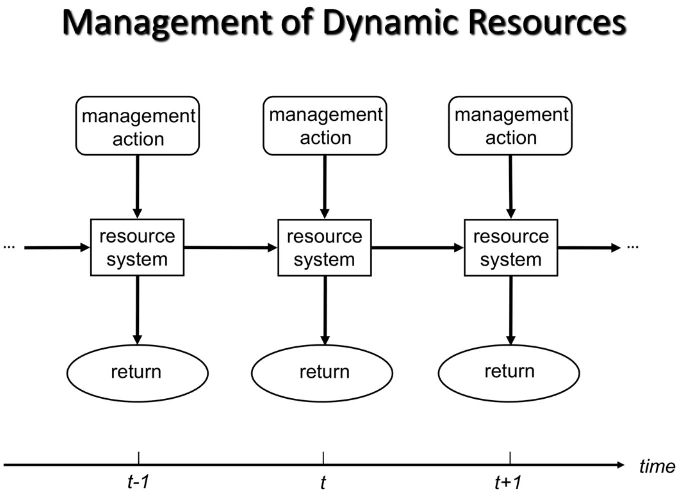

FIGURE 1
Diagram of a generalized recurrent decision process. A management action is selected and taken at each decision point (time step, *t*). The action leads to the production of returns (variables that are components of management objectives) and potential changes in the resource system itself. Note that objectives (and thus returns) may include functions of state variables that characterize the resource system (modified from Nichols and Williams, 2013).

models used for recurrent decision processes must predict immediate and subsequent returns, as well as system state for the next, and subsequent, decision points (Figure 1). For habitat management, models may need to predict both the effects of management actions on habitat and the effects of habitat change on the managed wildlife population or community.

Decision processes are frequently characterized by many sources of uncertainty. Four of these are often highlighted and should be incorporated into modeling when possible: *environmental variation, partial controllability, partial observability*, and *structural uncertainty*. Although the primary focus of SDM and ARM modeling is on the effects of management actions, environmental variables external to management actions may also influence system dynamics. If certain environmental variables are identified as important system drivers, they may be incorporated individually into models. Variation associated with environmental variables that are not explicitly modeled simply adds variation to model predictions.

Partial controllability refers to variation in the implementation of management actions. For example, habitat management actions such as prescribed burning may be based on very precise and specific instructions, but the actual habitat effects that these actions produce can exhibit substantial variation, depending on such factors such as wind, recent weather (vegetation dry or wet), extent of bare ground, and fuel load (e.g., Breininger et al., 2010).

Partial observability refers to the ubiquitous problem in studying wildlife populations and communities that we can hardly ever count individuals perfectly. Instead, our counts nearly always "miss" individuals present on surveyed sample units, such that we require estimation methods to deal with non-detection (e.g., Seber, 1982; Williams et al., 2002; Kery and Royle, 2015; Seber and Schofield, 2019). For many problems in conservation, focal populations and communities inhabit areas so large that they cannot be surveyed completely. These situations require spatial sampling, which also adds variation to estimates of state variables (e.g., Lancia et al., 1994, 2005; Thompson, 2002; Williams et al., 2002). Such variation naturally adds to the variance of predictions and should be accounted for when possible.

Structural uncertainty refers to imperfect knowledge of the manner in which systems respond to management actions. This uncertainty is sometimes expressed in the form of different discrete models of system behavior. Define a discrete model set as the models (usually small in number) considered to provide plausible descriptions of the dynamics of the managed system. Each model in the set is characterized by a model weight, reflecting the predictive ability of that model expressed relative to the other models in the set. Model weights sum to one for all the models in the set. We have more confidence in models with higher weights, believing them to be more likely to represent reasonable abstractions of the modeled processes. The weight of each model at a decision point determines its relative influence on the optimal decision. As the ARM process proceeds, weight should increase for model(s) that predict well and decrease for those that predict poorly (see *Learning*).

Another way to express structural uncertainty is by using parameters in a general model that permit a range of model behaviors. Such models are general with respect to the system response to management actions, such that different values of the parameters produce substantial differences in system response. As the ARM process proceeds and more observations are obtained, the estimated parameters should become more accurate (decreased bias and increased precision).

Monitoring in an ARM program serves the same three purposes listed above for any general SDM program. Monitoring 1) provides estimates of system state for making state-dependent decisions, 2) permits the manager to gauge the success of management, and 3) provides data used to develop and update management models. In ARM, monitoring is also 4) critical to learning, providing estimates to be compared against model predictions.

Decision algorithms provide a means of determining the "best" action based on the other process elements, where "best" is determined by the objectives. Decision algorithms can range from the thought processes of a manager to dynamic optimization programs. As noted above, recurrent decisions require consideration not only of expected returns for the current time step but also for all remaining steps in the decision process time horizon. Such decision problems can be solved using dynamic optimization approaches such as stochastic dynamic programming (SDP) (Bellman, 1957; Puterman, 1994). SDP deals with environmental variation and partial controllability, but not directly with the other two sources of uncertainty: partial observability and structural uncertainty.

An extension of SDP known as adaptive stochastic dynamic programming (ASDP) (Williams, 1996) projects both system and learning dynamics through time in order to determine optimal decisions for processes with structural uncertainty. Partially observable Markov decision process (POMDP) optimization was developed to deal with dynamic systems for which system state variables cannot be directly observed but must be estimated (Chades et al., 2021; Williams and Brown, 2022). The theoretical framework for dynamic optimization that can deal with all four sources of uncertainty has been developed (Williams, 2011; Fackler and Pacifici, 2014). SDP and ASDP have been used for most of the ARM programs implemented over the last 25–30 years in North America (Johnson et al., 1997; Martin et al., 2011; McGowan et al., 2015; Eaton et al., 2021; U.S. Fish and Wildlife Service, 2021).

ARM: deliberative phase

The deliberative or set-up phase of adaptive management entails the initial development of the above elements (Table 1). The establishment of objectives is a critical first step and requires attention to legal and regulatory considerations, as well as input from all relevant stakeholders for the managed system. Objectives are based on human values, and different stakeholder groups frequently differ in how they value any system. Workshops are sometimes held to obtain stakeholder input and to accomplish the difficult task of developing compromise objectives to which all stakeholders can agree. Scientists may be stakeholders, but their perspectives carry no extra weight in identifying objectives.

Deciding on a set of potential actions also requires substantial stakeholder input, as some actions (e.g., predator control) may be

TABLE 1 Operational steps in adaptive management include the development of ARM elements in the deliberative or set-up phase and the iterative process of making and implementing decisions.

Deliberative or set-up phase
1. *Objectives* Identify and clearly specify objectives agreeable to all relevant stakeholders
2. *Management actions* Identify a set of management actions with the potential to achieve objectives
3. *Models* Develop models for predicting system dynamics and responses to management actions, accounting for uncertainty
4. *Monitoring* Establish monitoring to estimate system state and other key variables
5. *Decision algorithm* Develop a clear approach to using elements 1–4 to decide which action should be selected at each decision point
Iterative phase
1. *Make decision* Select the management action that is “best” relative to objectives, using all of the elements of the deliberative phase
2. *Implement action* Apply the action to the system
3. *Monitor* Estimate system response and returns
4. *Assess/learn* Learn by comparing model-based predictions against observed system dynamics
5. *Return to iterative step 1* Next decision depends on new system state (from monitoring) and updated model weights (learning from last decision point)

deemed unacceptable for social or political reasons. Scientists may have a more substantial role than other stakeholders in developing a set of potential actions, as scientists sometimes have specific insights about the relative effectiveness of different actions.

Development of the other three elements—models, monitoring program, and decision algorithm—is typically carried out primarily by scientists and managers. Other stakeholders may be asked to contribute, but the technical aspects of these elements usually require specialized expertise. Technical experts are often organized into ARM working groups, which then report back periodically to the full stakeholder group. Models, monitoring, and the decision algorithm should be tailored to the specified objectives and actions. Examples of deliberative phase efforts for different ARM programs are provided by Johnson et al. (1997), Nichols (2000); McGowan et al. (2015), and Eaton et al. (2021).

ARM: iterative phase

The initial step of the iterative phase entails selecting a management action at the first decision point (Figure 1) using the decision algorithm with all the elements developed in the deliberative phase (Table 1). The selected action is then applied to the system, producing returns and driving the system to a new state.

The new system state is estimated before the next decision point via the monitoring program. The estimated state is compared against model-based predictions in order to update model weights or model parameters (see *Learning*). At the next decision point, a management action is selected using the decision algorithm and based on the objectives, actions, and models, all of which typically remain the same as in the first step, together with the new estimate of the system state and the updated model weights. The new action is applied, returns are accrued, and the system again moves to a new state. The iterative process proceeds in this manner (Table 1).

The iterative phase thus entails selecting actions that are good or optimal with respect to the specified objectives while simultaneously reducing uncertainty by learning which model(s) represents the best approximation to the processes governing system responses to management actions. This combination of wise decision-making and simultaneous learning distinguishes adaptive management from other forms of management.

Learning

Learning in ARM occurs via the incorporation into the decision process of a scientific step, entailing the comparison of model-based predictions against observations. When structural uncertainty is expressed as a set of discrete models, learning occurs via the updating of model weights via Bayes' theorem (e.g., Williams et al., 2002; Link and Barker, 2010). The updating is based on two sources of information for each model. The first source is the current (prior) weight, reflecting the relative predictive ability of each model based on past observations accrued up until the decision point. The second source of information is the probability of observing the current value of the system's state variable (as estimated via monitoring) under each model. The updating entails computing a new model weight (posterior) based on both the old weight and how well each model predicts the new data on the system state. If the model set includes a good approximating model, then the weight for that model should evolve to approach 1, whereas the weights of models that predict more poorly should eventually approach 0.

Model uncertainty can also be expressed using a very general model with one or more focal parameters, the values of which can produce models with very different behaviors. For example, we might have a model parameter for a habitat effect that can take any value between 0 and 1, with 1 indicating a maximal effect of the habitat manipulation and 0 indicating no effect. Such a model can be viewed as providing a continuous model set, and we reduce uncertainty by increasing the accuracy of the estimate of this parameter and its distribution. The updating of the distribution(s) of the parameter(s) again follows Bayes' theorem and includes the information about the distributions based on all data collected through time t (the prior distributions), as well as the new data (time t+1). The estimated distributions of these parameters are expected to become more and more accurate through time.

Learning in adaptive management is thus accomplished by this updating of either model weights or focal model parameters that specify structural uncertainty. Sometimes, a distinction is made between *active* and *passive* adaptive management. Under passive ARM, learning is an anticipated, but untargeted, by-product of management. In passive ARM, the dynamic decision algorithm uses the current state of knowledge to represent knowledge in all future points in the time horizon (Nichols and Williams, 2013). In active ARM, learning is anticipated and targeted, such that the management decision is based not only on the system state (e.g., abundance) and projections of it into the future but also on the current state of knowledge (e.g., model weights or parameter estimates) and projections of its future evolution. Active adaptive management thus addresses the "dual control" problem of balancing short-term benefits (immediate returns) with the long-term benefits that result from learning. Both approaches incorporate learning and then use what is learned to manage, essential features of adaptive management.

Double-loop learning phase

We have emphasized the importance of the deliberative phase in carefully establishing the various elements of the ARM process. However, the adoption of ARM does not mean that these elements cannot be modified at some later time in the process. Double-loop learning is the term used to indicate a phase of ARM at which one or more of the decision process elements are revisited and possibly revised (Williams et al., 2007; Williams and Brown, 2018).

Double-loop learning can be initiated for a variety of different reasons. For example, experience with the ARM process could produce changes in perspective that would lead to reconsideration and possible modification of objectives. New ideas may arise for additional actions that might be effective. If none of the models in the model set seems to predict well, then modifications or new models may be considered. Monitoring programs may be modified in efforts to produce more accurate estimates.

The temporal scale of double-loop learning is typically longer than that of the iterative phase of ARM. For example, the iterative phase may entail decision points every year. However, double-loop learning interventions often occur irregularly, for example, after 5 or 10 years of experience with the ARM process, if reconsideration of one or more of the process elements seems warranted.

ARM and habitat–population linkages

It is common in grant proposals and introductions to ecological papers to claim conservation utility for the proposed and reported work. It is true that any information about an ecological system has the potential to be somewhat relevant to conservation decisions for the managed system. However, it is also true that different kinds of information about a system can vary greatly in their utility to conservation. Our primary motivation for describing SDM and ARM is to provide a shared understanding of these processes and how they work in general. Using this framework, we next specify exactly how information about habitat–population linkages fits into these formal decision processes (see *Habitat management*). Specifically, when actions for an SDM or ARM process include habitat manipulations, models predicting the consequences of such actions for the managed system are required for informed decision-making. Such models will typically include submodels for predicting 1) the effects of actions on habitat and 2) the effects of habitat changes on the focal population (habitat–population linkages). It is our hope that knowledge of this use of habitat–population linkages will provide greater focus for those wishing to contribute to conservation via habitat management. A secondary motivation for this description of SDM and ARM is to create greater awareness of these formal approaches to conservation decisions, leading to good decisions now and to learning (reducing uncertainty) that allows even better decisions in the future.

Habitat management

A frequent objective in conservation biology and wildlife management is to increase or maintain the population size of a focal species. The management actions that can be used to achieve such an objective are usually very limited and frequently entail efforts to modify habitat, in a broad sense. For the purposes of this set of papers, we operationally define "habitat" as "the resources and conditions present in an area that produce occupancy - including survival and reproduction - by a given organism" (Hall et al., 1997).

Models for habitat management: general

SDM (including ARM) approaches to management require models to project responses of the focal population to the different management actions (Figure 1). Habitat management models developed for this purpose are frequently comprised of two submodels. First, we attempt to project the consequences of management actions on habitat itself. Second, we try to project the consequences of changed habitat for the focal population(s)—the topic of this special issue. This decomposition usually leads to models that include at least two state variables: one characterizing habitat and the other the focal population.

Models used for habitat management do not require the decomposition of focal processes as described above. We could model focal population responses to habitat management actions directly, but this less mechanistic approach may not be as useful in some respects. For example, if direct modeling of population response to habitat management provides poor predictions, then it may be more difficult to diagnose the reasons for the problem than if the two processes had been modeled separately. The poor performance could be attributed to the failure of the management action to affect habitat in the predicted way, the failure of the habitat change to affect the focal population as predicted, or a combination of both issues.

Models for habitat management: habitat responses to management

Models of habitat dynamics are used for projecting the consequences of management actions on the habitat state variable(s), where such variables are defined based on their relevance to the focal wildlife population(s). Such habitat models can focus on the processes governing habitat change, frequently parameterized as habitat state transition probabilities. For example, we might have one set of transition probabilities that govern changes in habitat state in situations with no habitat management (e.g., arising from natural successional processes) and another set of transition probabilities associated with the application of a management action to habitats of each specific state.

As a specific example, we consider management of Florida scrub and flatwoods habitat for the Florida scrub-jay, *Aphelocoma coerulescens*. Scrub-jay habitat can be classified by structural height into four classes: short (Sh), optimal (Op, the best habitat state for scrub-jays), tall-mix (Tm), and tall (Ta; see Breininger and Carter, 2003; Breininger and Oddy, 2004). For the purposes of scrub-jay management, habitat within a managed area can be subdivided into a grid of 10-ha cells (the approximate size of a scrub-jay territory). We define n_t^r as the number of patches (cells) in habitat class r at time t and transition probability ψ_t^{rs} as the probability that a habitat patch in state r in year t is in habitat state s in year t+1. Habitat dynamics can be modeled as a first-order Markov process governed by a matrix of transition probabilities:

$$\begin{bmatrix} n_{t+1}^{Sh} \\ n_{t+1}^{Op} \\ n_{t+1}^{Tm} \\ n_{t+1}^{Ta} \end{bmatrix} = \begin{bmatrix} \psi_t^{ShSh} & \psi_t^{OpSh} & \psi_t^{TmSh} & \psi_t^{TaSh} \\ \psi_t^{ShOp} & \psi_t^{OpOp} & \psi_t^{TmOp} & \psi_t^{TaOp} \\ \psi_t^{ShTm} & \psi_t^{OpTm} & \psi_t^{TmTm} & \psi_t^{TaTm} \\ \psi_t^{ShTa} & \psi_t^{OpTa} & \psi_t^{TmTa} & \psi_t^{TaTa} \end{bmatrix} \begin{bmatrix} n_t^{Sh} \\ n_t^{Op} \\ n_t^{Tm} \\ n_t^{Ta} \end{bmatrix}. \qquad (1)$$

We expect such transition matrices to differ for different habitat management actions. The probabilistic nature of habitat transitions reflects, among other things, the partial controllability of habitat management.

Inferences about habitat state transition probabilities are readily obtained from data on habitat classification of patches over time. Each habitat patch forms a row in a data matrix with columns identifying the different times (e.g., year 1, 2,…) they were visited. Habitat classes are the matrix entries specifying the habitat class of the patch at each sampling occasion during the study. Any of several software packages can then be used to estimate the ψ_t^{rs} and associated variances from such data. For example, if no patches become non-habitat and all patches can be located by investigators each time step (year), then multistate capture–recapture software (e.g., White and Burnham, 1999; Choquet et al., 2009) can be used to estimate transition parameters by setting survival and detection parameters equal to one. Loss of sites and non-detection can be dealt with as well. If habitat classification is based on remote sensing data, then misclassification may be an issue but can be handled if a subset of ground truth patches is available (Veran et al., 2012). Figure 2 provides a schematic diagram for a multistate model analysis of habitat dynamics in Florida scrub and flatwoods systems (Breininger et al., 2010).

In addition to the estimation of transition probabilities, analytic methods such as multistate capture–recapture and occupancy modeling also permit direct inferences about the potential influence of covariates on habitat transitions. For decision problems, these covariates can include management actions such as burning and mechanical cutting, leading to different transition matrices for different management actions. Examples of such analyses for Florida scrub and flatwoods systems are found in Breininger et al. (2009, 2010), Johnson et al. (2011), and Eaton et al. (2021), with the latter two references describing the incorporation of such modeling into decision processes.

In some situations, the classification of habitat into a small number of discrete states may not be feasible or as useful as simply focusing on a single habitat variable. In the case of Florida scrub-jay habitat, an important habitat variable for defining habitat quality is simply vegetation height (Breininger and Carter, 2003; Breininger et al., 2010). Thus, another approach to modeling would be to treat average vegetation height as a continuous variable, with different management actions (e.g., burning, mechanical cutting) predicted to decrease average height by different amounts. Scrub-jay survival and reproduction would then be predicted to be greater at intermediate heights and lower at shorter and taller heights.

Models for habitat management: population responses to management

The objectives of most programs of animal conservation and wildlife management focus on animal populations, and efforts to modify habitat provide one means of achieving such objectives. Although models of habitat change as a function of management actions are required by ARM, additional modeling is needed to specify focal population responses to changes in habitat, the focus of papers comprising this special topic. State variables frequently used in population management models include abundance, density, and occupancy. One way to draw inferences about population responses to habitat management is by observing static patterns of species abundance, density, or presence–absence in different locations characterized by different sets of habitat variables. However, such associations may not be good predictors of changes in abundance associated with habitat changes (e.g., Van Horne, 1983; Yackulic et al., 2015; MacKenzie et al., 2017). A more reliable approach is to address the effects of habitat on the vital rates governing population change (see Tyre et al., 2001; Yackulic et al., 2015).

Models most useful for management are also based on the effects of management actions on the vital rates governing state variable dynamics (Nichols, 2021). For example, assume that we are able to estimate abundance of a focal species in two different habitats within a system. If the system is in approximate equilibrium, then the estimated difference in abundance can be viewed as a measure of habitat effect. However, if we take a management action that converts a patch of one habitat type into the other, then we would not necessarily expect to predict the new abundance on that patch using the habitat effect. Instead, we would expect a period of transient dynamics as abundances changed in the direction predicted by the effect. When systems are not in equilibrium, the difference between abundances in patches of the different habitat types would not necessarily be useful in predicting abundance response to habitat changes either. However, when habitat effects on vital rates are estimated, then these effects can be used, together with estimates of current abundance, to directly predict abundance responses to habitat changes. In general, vital rates are used to predict time-specific changes in abundance resulting from any management action, absent any assumptions about equilibrium.

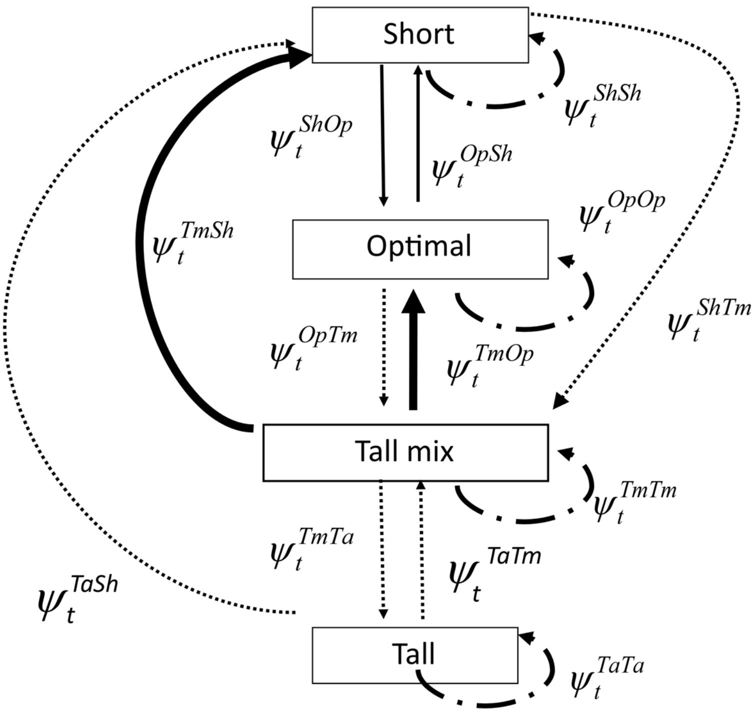

FIGURE 2
Transitions and associated probabilities estimated using a multistate model of scrub and flatwoods at Kennedy Space Center, Florida, 1994–2004 (Breininger et al., 2010). ψ_t^{rs} = probability that a patch in habitat state *r* at time *t* is in state *s* at time *t*+1, where *Sh* = short; *Op* = optimal; *Tm* = tall mix; and *Ta* = tall. Transitions depicted by heavy solid lines had adequate sample sizes for models including all covariates. Transitions depicted by thin sold lines occurred infrequently and were modeled using fewer covariates. Transitions with dotted lines had few occurrences and were modeled using only the covariate oak. Transitions from short to tall, optimal to tall, and tall to optimal never occurred and were constrained to zero. Transition probabilities for states that remained the same were estimated by subtraction (modified from Breininger et al., 2010).

The selection of data used to estimate system responses to changes in habitat depends on the system state variable(s) being modeled and on the methods chosen to estimate the variable(s) and associated vital rates. For example, there are many ways to estimate abundance, density, and vital rates (survival, recruitment, movement) that govern population dynamics (e.g., Seber, 1982; Williams et al., 2002; Royle et al., 2013; Kery and Royle, 2015, 2021; Seber and Schofeld, 2019). Many of the approaches for estimating abundance and density only require data from relatively short periods of time. Inferences about vital rates require multiple detections from individually marked individuals over longer time periods or, sometimes, temporal sequences of simple counts at multiple sampling locations (Dail and Madsen, 2011; Kery and Royle, 2021).

The occupancy state variable focuses on the presence or absence of a species in each of a set of specified sample units, and inference methods based on species-level detection–non-detection data are well-developed (MacKenzie et al., 2002, 2017). Similarly, methods are available for estimating the rates of local extinction and colonization from temporal sequences of detection–non-detection data across multiple sample units (MacKenzie et al., 2003, 2017).

Selection of analytic methods for estimating the effects of habitat on vital rates of animal populations is dictated by 1) the types of vital rates (hence, state variable) being considered, 2) the relative spatial scales of animal movement and habitat measurement, and 3) the relative temporal scales of habitat change and vital rate estimation. The relevance of identifying the appropriate vital rates stems from the need for reasonable samples of marked individuals for estimation of survival, recruitment, and movement using capture–recapture methods (e.g., Williams et al., 2002; Seber and Schofeld, 2019; Kery and Royle, 2021). If the scale of habitat assessment is relatively coarse, and if spatial sample units are large relative to the scale of animal movement, and if habitat change is very slow relative to study duration, then it may be reasonable to assume that animals remain associated with specific habitats for the duration of a study. In such cases, sample units may be grouped by habitat type, or habitat covariates can be measured for each unit, and tests for a habitat effect can be conducted using standard capture–recapture models for open populations (Pradel, 1996; Schwarz and Arnason, 1996). For example, Conway et al. (1995) used capture–recapture modeling to test for differences in overwintering survival between neotropical migrant birds in successional habitat vs. mature tropical forest in Belize but found survival to be very similar for the two habitat types. In addition to capture–recapture, inferences about survival and recruitment can also be drawn from raw counts of individuals in multiple sample units (Dail and Madsen, 2011; Kery and Royle, 2021) although this approach requires greater dependence on the selected model and its underlying assumptions.

If habitat remains relatively constant, but individuals move from one habitat type to another between sampling occasions, then capture history records of animals that are known to have moved can be manipulated and used with standard open-population capture–recapture models to draw inferences about associations between vital rates and habitat type (Franklin et al., 2000). However, multistate capture–recapture models were developed specifically for this situation of individual animal movement between sampling occasions (Arnason, 1972; Brownie et al., 1993; Schwarz et al., 1993; Lebreton et al., 2009) and are a natural choice. For example, Senar et al. (2002) used multistate models with capture–recapture data on the citril finch (*Serinus citrinella*) in a metapopulation containing one high-quality and one low-quality habitat in southern Spain. Birds in the high-quality habitat had higher survival rates, and movement from low- to high-quality habitat was greater than that in the reverse direction. While most studies focus on the habitat of patches inhabited by the focal species, multistate models can also be used to draw inferences about the effects of matrix habitat (occurring between patches) on rates of between-patch movement (Skvarla et al., 2004).

If habitat remains relatively constant over the period of study, but the scale of habitat assessment is very fine-grained such that animals are likely to move among multiple habitat classes frequently during a study, then near-continuous radio telemetry data may be required to properly estimate habitat-specific survival (Conroy, 1993; Conroy et al., 1996). In a radio-telemetry study of wintering American woodcock (*Scolopax minor*) in coastal Virginia, Conroy et al. (1996) used a proportional hazards approach (Cox, 1972, 1975) and found no apparent difference in daily survival rates between pine and hardwood habitats.

Data requirements for estimating probabilities of local extinction and colonization within an occupancy framework are generally less stringent than for estimation of survival and recruitment. Periodic surveys are used to collect species-level detection–non-detection data for the focal species on multiple sample units, and if habitat change is slow relative to study duration, units may be grouped by habitat type or characterized by a continuous habitat covariate. In an early application of this approach, Ferraz et al. (2007) investigated habitat fragmentation effects experimentally for 55 Amazon bird species in Brazil, finding strong evidence of a negative effect of patch size on local extinction probabilities.

Two general approaches can be used to investigate habitat–population relationships when habitat and the focal population exhibit dynamics operating at approximately the same time scale during a study. One approach is similar to that used for relatively static habitat, in the sense that habitat for each sample unit at each sampling occasion in the study is recorded and inserted as a standard covariate, absent any effort to model habitat dynamics. Multistate capture–recapture models can be used with changes of state induced by either animals moving or animals remaining in a sample unit, but habitat changing.

The other approach is to model habitat and population dynamics jointly. Breininger et al. (2009) used multistate capture–recapture models to estimate survival rates of Florida scrub-jays on breeding territories, with habitat state defined at each sampling occasion as short, optimal, tall-mix, or tall (see above). Survival was greatest for birds in territories with optimal habitat, as predicted. Territory habitat dynamics were modeled separately and used to conclude that most changes of habitat state experienced by birds resulted not from birds moving, but from birds remaining in territories that changed habitat state via natural succession or management action (e.g., burning). So, both habitat and population dynamics were modeled, and the next step would be to directly link the two models using a joint likelihood. The advantages of a joint likelihood include the ability to deal with potential misclassification of habitat (or missing values) in certain sampling occasions. In addition, joint likelihoods admit reciprocal relationships in which wildlife populations can also influence habitat dynamics (as with some grazing systems), and provide a natural approach for the direct estimation of variances associated with habitat–population relationships.

Joint likelihoods can also be developed for the occupancy state variable, permitting simultaneous modeling of population and habitat dynamics (MacKenzie et al., 2011). As an example, MacKenzie et al. (2011) surveyed seasonal pools for spotted salamander (*Ambystoma maculatum*) egg masses in Canaan Valley National Wildlife Refuge (NWR), West Virginia, for the purpose of investigating the potential effects of pool size (based on the surface area of water) as a habitat variable. The probability that a pool with no egg masses (no breeding) in breeding season t was colonized and had egg masses in t+1 was greater for pools that were larger in t+1. The probability that a pool with egg masses in year t again had egg masses in year t+1 was also greater for pools that were larger in year t+1.

Investigations may also include multiple habitat variables that differ with respect to the temporal scale of their dynamics. Miller et al. (2012) investigated the occupancy of the arroyo toad (*Anaxyrus californicus*) in southwestern California focusing on the effects of two habitat variables: watershed class and water availability. Watershed class referred to areas populated by mostly ephemeral or mostly perennial streams, and this classification did not vary during the study. Sample units were stream segments within watersheds and were classified as unsuitable (dry) or suitable (containing water) each breeding season. This aspect of habitat suitability was highly dynamic throughout the study and modeled as a first order Markov process that was linked with toad occupancy dynamics. Inferences were available about the effects of both habitat variables on local extinction and colonization of toads.

In summary, there are multiple analytic approaches for investigating the relationships between habitat variables and population dynamics. Such relationships underlie any attempt to manage populations by managing their habitat and must be incorporated into models used in decision processes such as SDM and ARM. Models of habitat effects on population vital rates are expected to be more useful to management than models describing the relationships between habitat and static state variables. Multiple approaches are available for drawing inferences about these habitat–population relationships, and selection of the most appropriate approach for a study depends on the selected state variables and vital rates, the rate of habitat change relative to study duration, and the rate of animal movement relative to study duration and habitat change.

ARM for habitat management: an example

We describe a program of adaptive habitat management for the Florida scrub-jay inhabiting scrub and flatwoods habitat in coastal Florida. As described above, habitat in this system can be divided into classes based on vegetation height and value to scrub-jays. For the purposes of the scrub-jay ARM program, habitat of optimal height in previous classifications was further classified as either optimal-open (containing numerous patches of open sand) or optimal-closed (sand patches grown over by encroaching vegetation), producing five overall habitat classes: short, optimal-open, optimal-closed, tall-mix, and tall. These five habitat classes can be located on soils characteristic of either scrub or flatwoods, providing one other habitat variable relevant to transitions of both habitat class and scrub-jays.

Scrub-jay population growth is greatest in the optimal-open habitat class (Breininger and Carter, 2003; Eaton et al., 2021), which represents a transitional stage of natural vegetative succession in this system. Alterations in the natural fire regime caused by human land-use changes over the last half-century in Florida's Atlantic coast have resulted in significant losses of open scrub and flatwoods habitats with a transition to taller scrub and fire-resistant forests (Duncan et al., 1999; Duncan and Schmalzer, 2004). The management problem is thus one of maintaining enough optimal habitat to permit the maintenance and growth of Florida scrub-jay populations. However, habitat management actions (burning and mechanical cutting) do not usually lead directly to optimal habitat. Instead, these actions can increase the probabilities that tall-mix and tall habitat transition to short habitat, which can then transition to optimal-open habitat in subsequent years. So, despite the availability of potentially useful management actions, the problem of creating and maintaining enough optimal-open habitat to promote scrub-jay population growth is a difficult one.

The 1990s and early 2000s were characterized by a general concern for the loss of good scrub and flatwoods habitat in coastal Florida and the consequent problems for scrub-jay populations. An adaptive habitat management program for Florida scrub-jays was developed for Merritt Island National Wildlife Refuge and the Kennedy Space Center (Johnson et al., 2011). This ARM program was not fully implemented, but aspects of it were viewed as successful, and it provided a blueprint for subsequent efforts.

In the early-mid 2000s, Brevard County community leaders, land managers, and local biologists expressed interest in developing an ARM program for the mainland ecosystem. Potential stakeholders were identified and invited to two workshops in 2006 to discuss the idea of developing an ARM program for scrub and flatwoods habitat directed at Florida scrub-jays (Eaton et al., 2021). The positive response to these initial workshops led to a decision to develop an ARM program in Brevard and Indian River counties. As part of the deliberative phase of ARM, subsequent workshops proceeded with program development, focusing on eliciting management objectives, identifying alternative actions, developing preliminary hypotheses and associated models, and establishing a monitoring program. The iterative phase of the ARM program was implemented in 2012, with results through 2018 summarized by Eaton et al. (2021).

The overall objective of this scrub-jay ARM program was to maximize the number of 10-ha grid cells (the approximate size of a scrub-jay territory) within managed land units that were occupied by scrub-jays. The larger management units were areas administered by different agencies or land ownership groups. The four potential management actions were identified as follows:

1. Burn (BRN): the use of prescribed burning with high-intensity fires generally applied when vegetation is low enough to carry fire, often during the growing season;
2. Light mechanical cutting, followed by burn (LMB): the targeted spot-cutting of taller, less flammable vegetation, followed by a prescribed burn within 3 months;
3. Heavy mechanical cutting, followed by burn (HMB): a more intensive mechanical treatment than LMB in sites where vegetation is beyond the height to perform a fire;
4. No action (NONE): no management action.

The ARM process entailed selecting one of these actions for each 10-ha cell each year.

The modeling for this ARM program included one submodel for habitat responses to management actions and another submodel for scrub-jay responses to habitat. Both submodels were developed at the 10-ha cell level. For habitat state, there were 5 × 5 transition probability matrices for each soil type (scrub, flatwoods) and each management action, producing 8 matrices and 200 transition probabilities. These transition probabilities provided a natural way to incorporate the partial controllability of scrub-jay habitat management. During the deliberative phase, managers and knowledgeable stakeholders were asked to provide their estimates for each of these 200 transition probabilities, and elicited estimates were used to develop pseudo-observations that provided the prior distributions for these initial transition matrices (Eaton et al., 2021). Subsequent values for these transition matrices were obtained by updating based on new monitoring data each year.

A dynamic occupancy model (MacKenzie et al., 2003, 2017) was developed to model scrub-jay dynamics. Cell-level probabilities of local extinction and colonization were modeled as functions of habitat state, neighborhood cell occupancy (an autologistic effect; Augustin et al., 1996; Yackulic et al., 2012; Eaton et al., 2014), and overall system occupancy. The neighborhood and overall occupancy levels (proportions of cells occupied by scrub-jays) were included because of their potential influence on probabilities of cell-level colonization (sources of colonists) and extinction (via the rescue effect; Brown and Kodric-Brown, 1977). Initial occupancy levels were estimated directly from monitoring data, and the habitat effect parameters were initially estimated based on expert elicitation from the group of managers and then updated with monitoring data as the program proceeded.

Many of the land managers participating in the program were already doing some level of habitat and scrub-jay monitoring prior to the program. A monitoring protocol for ARM was developed to ensure that the needed information was being collected each year. In cases where the land managers were unable to monitor, other program biologists carried out these tasks.

Optimal state-dependent decisions were obtained beginning in 2014 using modified stochastic dynamic programming approaches (Miranda and Fackler, 2002; Fackler, 2012). A passive adaptive management approach was used, such that the optimization was based on anticipated system responses to management and not on anticipated learning. Efforts were made to share the recommended actions with the set of land managers, but carrying out these recommendations was difficult and inconsistent. These difficulties resulted from several factors, including 1) the numerous different land managers involved and their different levels of resources to devote to management, 2) the fact that most land managers had multiple management cells with different actions recommended for different cells, and 3) some recommended actions (e.g., those that included fire) could not always be applied because of the absence of suitable weather conditions during the appropriate time periods. Thus, the recommended optimal actions were not applied at all times and to all sites. However, this did not preclude learning, as an action (recall that the action set included "none") was taken at every cell in every year, responses of habitat and scrub-jays were estimated via monitoring every year, and these data were used with model predictions for annual parameter updating.

The deliberative phase of this ARM program was quite long, extending from approximately 2006 to 2012–2014. We believe that the main reason for this was the increased difficulty in bringing the stakeholder group together and eliciting objectives, actions, values of parameters for prior distributions, etc., from such a diverse group, as opposed to a more streamlined situation with a single agency and decision-maker. Indeed, this is the first ARM program that we know of to have been developed successfully by a consortium of public and private landowners and stakeholders.

The iterative phase of ARM then proceeded as described in general above. Management actions were carried out at sites, resulting habitat and scrub-jay changes were identified by the monitoring program, and transition parameter estimates for both habitat and scrub-jays were updated each year using this new information. Precision of habitat and scrub-jay transition probability estimates increased through the years of the ARM program, and the dissimilarity of the sets of annual estimates decreased with time as well. Both of these trends provide evidence of learning about these key management parameters during the ARM program. Learning was also consistent with *a-priori* hypotheses, with greater probabilities of scrub-jay colonization and occupancy and lower probabilities of extinction, associated with optimal habitat and with greater system-wide occupancy. Scrub-jay colonization probabilities were higher for cells with more occupied neighbors as well. The general consistency of new results for scrub-jays with predictions was expected because of the substantial research previously conducted on this species. Some predictions about action-specific habitat transitions were supported, whereas others were not, emphasizing the importance of dealing with uncertainty even for well-studied systems.

With respect to management of the system, the number of optimal-open cells increased modestly over the course of the program, and the number of tall-mix and tall habitat cells decreased, reflecting success in habitat management. The proportion of cells occupied by scrub-jays did not increase over the 2013–2018 period, emphasizing the difficulty associated with managing this species using this type of habitat management. Specifically, the habitat management actions for suboptimal tall and tall-mix states increased transitions of patches to the short state (also suboptimal), and short state patches eventually grew to the optimal state. However, the time spent by patches in suboptimal states, even post-management, presents a substantial difficulty. Recognition of this difficulty is an important result, in this case leading to consideration of new potential management actions. More generally, the results of this ARM program emphasize the importance of recognizing the limits of some management actions and directly assessing via monitoring, rather than assuming, the effects of management (e.g., Nichols, 2012).

Summary and conclusions

SDM provides a general framework for virtually any decision process. ARM is a special case of SDM developed for recurrent decisions characterized by potentially resolvable uncertainty. In the iterative phase of ARM, periodic decisions are made based on objectives, potential actions, models of system response to actions, system monitoring, and a decision algorithm. Models, such as those linking habitat quality to population dynamics, are important in providing predictions about which action will be "best" at achieving objectives. Model uncertainty impedes decision-making but is the focus of ARM and is addressed by incorporating a scientific step directly within the overall management process.

Linking habitat quality to population dynamics for conservation decision-making, the theme of this group of papers, primarily concerns the development of models to predict population responses to habitat management. A logical way to think about this modeling entails two steps: 1) linking management actions to habitat dynamics and 2) linking habitat dynamics to population dynamics. We describe one way to model habitat dynamics using matrices of habitat state transition probabilities, with different matrices associated with different management actions. We argue that the linkage of habitat dynamics to population dynamics is best accomplished by linking habitat and habitat change to population vital rates. We further argue that the selection of methods used to estimate the effects of habitat on population vital rates should be based on 1) the types of vital rates (and state variable) being considered, 2) the relative spatial scales of animal movement and habitat measurement, and 3) the relative temporal scales of habitat change and vital rate estimation. We outline modeling approaches appropriate for different scenarios.

In order to illustrate how this modeling is incorporated within a management program, we describe an example program of habitat management focusing on the Florida scrub-jay, a species that relies on a transitional stage of natural habitat succession. Decreases in natural disturbance (fire) over the last half-century have produced decreases in the amount of habitat in this transitional stage, motivating habitat management efforts. An ARM program was developed to make good decisions for this recurrent decision problem and to simultaneously reduce uncertainties that impeded good decision-making. Models were developed to predict habitat transitions as a function of management actions and scrub-jay population dynamics as a function of habitat state. These predictions informed annual decision-making. In addition, a monitoring program provided information on both habitat and population dynamics, permitting the updating of key model parameter estimates (i.e., learning) and the use of the updated models to make subsequent decisions.

It is very common for studies of habitat to claim a conservation motivation. However, conservation requires the selection of actions that will increase the likelihood of attaining program objectives, and explanations of exactly how habitat study results will be used to make those decisions are rare. We believe that SDM and ARM provide frameworks that should be useful in making decisions about habitat management. In particular, these frameworks specify exactly how models linking management to habitat, and habitat to population dynamics, are incorporated into the decision process. We believe that models that are developed in the context of these frameworks, and with explicit knowledge of their uses within these frameworks, are most likely to be useful in developing decisions about habitat management.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

JN: Writing – original draft, Writing – review & editing. DB: Writing – original draft, Writing – review & editing. DA: Writing – original draft, Writing – review & editing. RL: Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Linking PVA models into metamodels to explore impacts of declining sea ice on ice-dependent species in the Arctic: the ringed seal, bearded seal, polar bear complex

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Arctic ecosystems are especially vulnerable to the impacts of climate change because of the limit to possible northward shifts for species dependent on land or continental shelf and because the rate of warming of the region has been 2-4 x the global average in recent decades. The decline in sea ice in the Arctic has both direct and indirect impacts on the species that live in association with ice, breeding on it, traveling over it, feeding on other ice-dependent species or avoiding competition with subarctic species that cannot exploit resources in ice-covered areas. Herein, we present a metamodel of a top-level predator, the polar bear (*Ursus maritimus*), and two of its key prey species, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), which are important in maintaining current polar bear densities and in turn are strongly influenced by bear predation. We used a metamodel that links Population Viability Analyses of the three species in order to examine how the impacts of declining spring land-fast sea ice on the fjords of Svalbard (Norway) and Frans Josef Land (Russia) can cascade through this predator-prey system. As the ice conditions that allow ringed seals to raise pups in snow-covered lairs on the frozen fjords diminish, or even disappear, ringed seal populations using the land-fast sea ice will collapse due to lack of successful recruitment. Consequently, the polar bear population, which relies heavily on hunting ringed seals in the land-fast sea ice to be able to raise their own offspring is also likely to decline. Our models suggest time-lags of decades, with the polar bear population not entering into decline until the lack of recruitment of ringed seals results in the depletion of breeding age ringed seals – starting in the third decade from the start point of the model and dropping below the initial population size only some decades later. Although lags between climate change and impacts on the ice-associated fauna are expected, the sea ice conditions have already changed dramatically in the northern Barents Sea region, including the Svalbard Archipelago, and the collapse of this Arctic species assemblage might already be underway.

KEYWORDS

Arctic, climate change, ringed seal, polar bear, bearded seal, population viability analysis, metamodel

1 Introduction

Global warming is impacting species across the globe (Pacifici et al., 2015; Stanton et al., 2015; Scheffers et al., 2016; IPCC, 2023), but Arctic endemic species are especially vulnerable to the ongoing warming, because of: 1) the limit to possible northward expansion for species dependent on land or continental shelf waters, 2) their inherent physiological adaptations to cold temperatures, 3) their conservative life-history strategies (long life-times and low reproductive rates), designed to buffer interannual variation and 4) their ecological dependencies on snow/ice, and 5) because the rate of warming in this region is two to four times the rate of the planet as a whole (Gilg et al., 2012; Previdi et al., 2021; Rantanen et al., 2022; Shu et al., 2022; Taylor et al., 2022).

The ongoing declines in sea ice in the Arctic are a particularly visible sign of global warming, which has dramatic implications for sympagic (ice-dependent) communities. IPCC's 6th assessment suggested that the Arctic could experience ice-free conditions in September prior to 2050 (IPCC, 2023). Other recent projections suggest that it is likely that these conditions will be experienced in the next decade or two (Kim et al., 2023; Jahn et al., 2024). Arctic marine mammals use sea ice in diverse ways that include seeking refuge from open water predators, in order to travel over long distances (without swimming in the case of polar bears), for feeding on other ice-dependent species (invertebrates, fish, marine mammals), to reproduce, molt, rest and also to avoid competition with subarctic species that cannot exploit resources that occur in ice-covered areas (ACIA, 2005; CAFF, 2013, 2017; Meredith et al., 2019; AMAP, 2021; Kovacs et al., 2021a).

All Arctic endemic marine mammals are strongly ice-affiliated and hence are threatened by both the direct effects of habitat loss and the indirect effects of sea ice losses on Arctic marine food webs and concomitant human activity increases in areas previously protected by ice cover (Tynan and DeMaster, 1997; Regehr et al., 2007; Laidre et al., 2008, 2015; Kovacs et al., 2011, 2012, 2021a; Reeves et al., 2014). Populations of some currently abundant species are likely to decline (or even be regionally extirpated), and because marine mammals are key species in Arctic food webs, there will likely be secondary impacts on species that prey upon them, are preyed on by them, or compete with them (Blanchet et al., 2019; Kiszka et al., 2015). Because of their strong affiliation with sea ice, Arctic marine mammals are seen as sentinels of Arctic Ocean health (see Moore and Gulland, 2014). Some climate change impacts on marine mammal populations have been demonstrated (e.g. Udevitz et al., 2012; Stenson and Hammill, 2014; Øigård et al., 2014; Rode et al., 2022; Vacquiè-Garcia et al., 2024), but logistics challenges and costs of surveys and other data acquisition for these animals have created a lack of base-line comparative data for many populations/species, making it difficult to document or accurately predict trends (see Kovacs et al., 2021a for a review).

Attempts to predict effects of climate change on species fall into three broad categories (Dawson et al., 2011; Pacifici et al., 2015; Willis et al., 2015; Foden and Young, 2016): descriptions of species and habitat traits that make species more vulnerable (e.g., Laidre et al., 2008; Foden et al., 2013); a correlative approach that models shifts in species distribution based on observed niche and projections of future suitable ranges (e.g., MacLeod, 2009; Gregory et al., 2012); and mechanistic models of the effects that climate change will have on physiological or population processes (e.g., Molnár et al., 2010, 2011). These approaches have increasing specificity, and therefore would be expected to provide more accurate predictions as the detailed mechanisms through which climate change affects species are examined. However, as models become more specific, they typically also become more narrowly focused, and therefore can omit interactions between species or other environmental processes that might be essential for the persistence of the focal species. Some studies have combined aspects of several of these approaches to obtain more integrated and complete analyses (e.g., Keith et al., 2008; Fordham et al., 2013a, 2013b; Foden and Young, 2016). Most analyses of this sort are theoretical, and few have been applied to marine mammal species.

Population Viability Analysis (PVA) is an approach that was developed to assess multiple interacting threats that have impacts on a species simultaneously. PVA uses demographic modeling, often in combination with genetic, habitat, and other models, to assess the risks to wildlife populations under various scenarios and evaluate the likely efficacy of protection, recovery, or restoration options (Shaffer, 1990; Boyce, 1992; Beissinger and McCullough, 2002; Morris and Doak, 2002). PVA models have been used to examine pending impacts of climate change on species (e.g., Wichmann et al., 2005; Molnár et al., 2010; Molano-Flores and Bell, 2012), but these studies have generally employed the standard PVA approach of focusing on a single species and its habitat. Thus, they consider other species with which the focal species interacts as not themselves to be undergoing changed population dynamics due to climate change, or at least as being independent systems rather than being tightly coupled with the critical interactions being modified by climate. Even in studies that might be termed multi-species PVAs, addressing climate change or otherwise, usually independent analyses are completed on a set of species. However, if it is the species interactions that are dependent on climatic conditions, then single-species PVA models will often fail to identify the disruptions to ecological communities that will be caused by climate change. However, species focused PVA models can be combined into "metamodels" of tightly interacting species, by linking a PVA model for each species to others, so that the dynamic change in each species can affect the others (Lacy et al., 2013). Each species model can be impacted by common or separate external environmental drivers, and emergent properties of the community's dynamics can emerge from the metamodel. In such a way, PVA has recently been extended to examine predator-prey interactions (e.g., Shoemaker et al., 2014), impacts of invasive species (Miller et al., 2016), disease-host interactions (e.g., Bradshaw et al., 2012; Wells et al., 2015), and multiple concurrent threats (Prowse et al., 2013).

Herein, we present a metamodel for a top-level predator, the polar bear (*Ursus maritimus*), and two of its prey species, ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) that are important to the persistence of the polar bear and in turn are strongly influenced by bear predation. The interactions between these species, as well as other aspects of the biology of each species, are highly dependent upon sea ice. Therefore, changing Arctic sea-ice conditions as the climate continues to warm are likely to have especially profound impacts on the interdependence of these animals. We focused on the populations of the three species around the Svalbard Archipelago (Norway), Franz Josef Land (Russia), and the Barents Sea between these archipelagos, northward to the Arctic ice cap. These High Arctic areas have until recently had extensive ice cover, including the fjord areas within the archipelagos and coastal areas, throughout much of the year. But Svalbard in particular has changed dramatically, with rapid increases in air temperature and reductions in sea ice cover, along with intrusions of Atlantic Water masses (which are increasing in temperature) into the fjords especially on the west side of the archipelago (e.g., De Rovere et al., 2022; Isaksen et al., 2022; Urbanski and Litwicka, 2022). This region is experiencing warming at a rate twice the average for the Arctic, so is a bellwether for other regions (Isaksen et al., 2022). We used a metamodel that links PVAs of the three species in order to examine the impact of declining spring-time land-fast sea ice on the fjords cascades through this predator-prey system. We modeled the ringed seals as the primary prey species; its relationship with polar bears is likely to be strongly influenced by changing ice conditions. We modeled the bearded seal population as an alternative prey for which predation might not be as strongly impacted by changing ice conditions. This metamodel therefore allows us to project possible severity and timing of some climate change induced threats to these Arctic endemic species.

2 Methods

2.1 PVA models

Population models for each of the three species were developed with the Vortex PVA software version 10.6 (Lacy, 2000; Lacy et al., 2023; Lacy and Pollak, 2023; program and manual available at https://scti.tools/vortex). Vortex is an age and sex-structured population model that simulates demographic processes subjected to both deterministic forces and demographic, environmental, and genetic stochastic events. Vortex simulates a population by stepping through a series of events that describe an annual cycle, including mate selection; reproduction; mortality; and dispersal. Each demographic rate can be specified to be a function of individual traits (e.g., age and breeding history), population characteristics (e.g., density and age structure), or external drivers (e.g., habitat characteristics). Vortex is normally used as an individual-based model, projecting population dynamics from the aggregate of fates of individuals, but it has an option to run as a simpler population-based model (analogous to matrix models of demography; Caswell, 2001) with any effects of individual variation around demographic rates assumed to be described adequately by the population means. In either mode, the simulations are iterated to generate the distribution of fates that the population might experience.

Demographic rates for the PVA models were obtained from published sources or, when data were lacking, from expert opinion of the authors and colleagues with validation that derived population statistics such as age structure and population growth rates consistent with the species biology and information on the local population. When available, we relied on data on the respective Svalbard populations; otherwise, we used information from other populations for the actual species. Variation in probabilities of demographic events caused by fluctuations in the environment across years ("environmental variation", EV, as opposed to directional trends in rates) is modeled in Vortex by sampling the demographic rates each year from binomial distributions with user-specified means and standard deviations. For our models we assumed that fluctuations in annual survival and reproduction are largely affected by the same factors, and we therefore specified that the correlation between reproduction and survival was 1.0 in each of our scenarios. This might exaggerate the annual fluctuations in population demography slightly, compared to a case in which fluctuations in survival and reproduction are independent. However, with species as long-lived as the Arctic seals and the polar bear, environmental variation will be unimportant to long-term projections because fluctuations in demographic rates average out across years. The initial age distributions were set at the stable age distribution calculated from initial fecundity and survival rates. However, the precise age distributions that arise from the complex metamodel dynamics often cannot be calculated analytically, and the first 2 or 3 years of projections sometimes display short-term fluctuations before long-term patterns emerge.

For ringed seals and bearded seals, the models were run as population-based simulations, with no considerations of individual characteristics that might modify fecundity and survival rates. For the polar bears, the Vortex model was run as an individual-based simulation, so that we could include the dynamics of females being available to breed only when they did not have dependent cubs (see below).

2.1.1 Ringed seal population and demography

Ringed seals in the Barents Sea give birth primarily on land-fast sea ice along the coastlines of Svalbard (Norway) and Franz Josef Land (Russia) (Kovacs and Lydersen, 2006). Some pupping is known to occur in the drift ice of the northern Barents Sea (Kovacs and Lydersen, pers. obs), but these areas have never been systematically surveyed. Female polar bears that den on the islands of the Svalbard and Franz Josef Land archipelagos rely heavily on feeding on ringed seals in land-fast sea ice breeding areas upon emergence from their dens in spring, after a long period of fasting in the den (Freitas et al., 2012). Their cubs are small and cannot travel great distances easily and cannot be immersed in water for long periods (Lone et al., 2018). Therefore, we assume that the number of ringed seals breeding on the land-fast sea ice is a critical determinant of the number of polar bear cubs that can be successfully raised.

The total population size of ringed seals in the Barents Sea region was set in our models at 200,000 in the non-breeding season based on surveyed areas in Svalbard and estimated densities in various breeding areas (Lydersen et al., 1990; Lydersen and Ryg, 1991; Smith and Lydersen, 1991; Krafft et al., 2006). These densities were extrapolated to apply also to the land-fast sea ice areas in Franz Josef Land. At the start of the simulation model, we divided this number of seals equally between those that use the land-fast sea ice around the archipelagos and those that use the vast areas of drift ice. A population of this size would produce about 54,000 pups per year (given reproductive rates below), about half of which would be raised on land-fast sea ice in fjords, with approximately half of these pups being born in Svalbard (rather than Franz Josef Land).

Ringed seals are physiologically mature (capable of spermatogenesis or ovulation) at a mean of 4.2 y and 3.5 y for males and females, respectively (Krafft et al., 2006), although maturation was about a year later in the 1980s, and successful breeding might not take place until a year or more after sexual maturation. Lydersen and Gjertz (1987) reported that 63% of males are sexually mature by age 6 y, and 60% of females are sexually mature by 5 y. We therefore modeled the reproductive lifespan of females is from 5 y to 40 y, with males starting to breed about 1 y later (at 6 y).

Most adult female ringed seals produce a single pup each year, with ovulation rates reported to be 91% (Lydersen and Gjertz, 1987) and 86% (Krafft et al., 2006) in Svalbard. We therefore specify in the model that 90% of adult females pup in an average year (with environmental variation across years, EV, of ± 5% SD). Ringed seals are polygynous, with younger and small males and old males being excluded from prime mating areas (Krafft et al., 2007). We assumed that the sex ratio of newborns is 1:1.

Survival rates for ringed seals have not been documented, so we used values that yield population growth rates (r = 0.059) and age structures that are plausible for the species. For females, we specified annual mortality rates of 50% (± 3% SD), 15% (± 1% SD), 12% (± 1% SD), 9% (± 1% SD), 7% (± 1% SD), and 5% (± 1% SD), for the first year, 2nd, 3rd, 4th, 5th, and later years, respectively. For males, we specified annual mortality rates of 50% (± 3% SD), 15% (± 1% SD), 12% (± 1% SD), 9% (± 1% SD), 6% (± 1% SD), and 5% (± 1% SD), for the first year, 2nd, 3rd, 4th, 5th, and later years, respectively. The maximum age for both sexes was set to 45 y (Lydersen and Gjertz, 1987), although fewer than 2% would be expected to live beyond 35 y based on the average annual mortality.

In order to model the interaction of polar bear and prey population dynamics, the annual mortality rate for each age class was divided into mortality attributable to polar bear predation (which will change during the simulation as the ratio of bears to seals changes) and the component due to other sources of mortality (which are assumed to remain constant over time). The mortality of each age class due to polar bear predation was calculated as the number of ringed seals preyed on by polar bears to meet the bears' energetic demands (see below), multiplied by the proportion of predation occurring on that age class of seals, divided by the number of ringed seals in that age class. The background annual mortality without bear predation was then calculated so that the survival prior to bear predation multiplied by the survival rate due to predation was equal to one minus the total mortality rates listed above. (See annotated input files in the Supplementary Material for further details and equations.) After removing the estimated predation by polar bears, the remaining non-bear mortality rates for females were 29.9%, 0%, 0%, 5.9%, 3.8%, and 1.8%, for the first year, 2nd, 3rd, 4th, 5th, and later years, respectively, and for males they were 29.9%, 0%, 0%, 5.9%, 2.8%, 1.8%, and 1.8%, for the first year, 2nd, 3rd, 4th, 5th, 6th, and later years, respectively. Our calculations of the numbers of 2nd and 3rd year ringed seals killed by bears amounted to the total mortality we had estimated for these two age classes. It is implausible that all mortality of these age classes was due to bear predation, so either some of the bear predation allocated to 2nd and 3rd year seals must be on other juvenile age classes instead, or our estimates of the total mortality experienced by other pre-reproductive age classes included some mortality that should be assigned to 2nd and 3rd year seals. However, given that the total survival to the age of breeding is the important factor in demographic projections determining population growth, the allocation of mortality among specific pre-breeding age classes does not affect population trajectories. The total mortality up to breeding age in our model was 36.5% without bear predation and 68.3% with bear predation.

The carrying capacity (K) was set to 125% of the initial population size for each subpopulation (land-fast sea ice vs drift/pack ice), to allow for population growth to be apparent in any scenarios with optimistic conditions, such as no decline in land-fast sea ice. It is not known to what extent ringed seals move between the areas around the archipelagos and the pack ice, but there are some fragmentary data that suggest high site fidelity in this species (McLaren, 1958; Smith and Hammill, 1981; Kelly and Quakenbush, 1990; Freitas et al., 2008; Kelly et al., 2010; Hamilton et al., 2015, 2016). Dispersal between the two areas was therefore modeled as occurring with 5% of subadults (ages 3y, 4y, and 5y) of both sexes moving to the other area each year. Alternative dispersal rates of 0% to 10% per year were also tested.

Key demographic parameters for the ringed seal populations are summarized in Table 1. Complete listing of the values entered into the Vortex population model are provided in the annotated input in Supplementary Material.

2.1.2 Bearded seal population and demography

No surveys have been undertaken for bearded seals in the northern Barents Sea, and the population is widely dispersed at variable densities throughout the area (Ahonen et al., 2017; Llobet et al., 2023). We set the total population size of bearded seals in the region at 50,000 in the non-breeding season.

Bearded seals become sexually mature at about 5 y for females and 6 y for males (Andersen et al., 1999), and we assumed that they typically produce their first pup at age 6 y. They can breed throughout a lifetime that can extend to 25 y. Most adult female bearded seals produce a single pup each year, and we specified in the model that 90% (with an EV of ± 5% SD) of adult females give birth in an average year. Bearded seals are polygynous (Van Parijs et al., 2003). We assumed that the sex ratio of newborns is 1:1.

Survival rates for bearded seals have not been documented, so we used values that yield exponential population growth rates (r = 0.048) and age structures that are plausible for the species. For both sexes, we assumed annual mortality rates of 25% (± 3% SD) in the first year and 10% (± 1% SD) each year thereafter. These mortality rates would result in a 6% probability of an animal surviving to the maximum age of 25 y. The annual mortality rate for each age class was divided into mortality due to polar bear predation and a second component arising from other sources of mortality. After removing

TABLE 1 Key demographic parameters used to model ringed seal population in the northern Barents Sea.

Parameter	Estimate	Source	Predicted effects of climate change
1st age of female reproduction	5y	Field	
1st age of male reproduction	6y	Field	
Oldest reproduction	40y	Expert opinion	
% adult females producing pups	90%	Field	Could be reduced if mating is disrupted due to reduced land-fast ice
Litter size	1	Field	
Maximum age	45y	Calculated from mortality rates	
Pup mortality	50%	Expert opinion	Increased due to lack of lairs on snow-covered land-fast ice, and consequent higher predation
Subadult annual mortality (age 1-2, 2-3, 3-4, 5-6)	15%, 12%, 9%, 6%	Calculated to fit population growth rate and age distribution	
Adult annual mortality	5%	Calculated to fit population growth rate and age distribution	
Current population size	200,000	Field surveys; extrapolation	
Maximum population size	250,000	Estimate to allow for some growth	
Proportion on Sv-FJ	0.50	Expert opinion	Reduced due to population decline on Sv-FJ
Archipelago-Pack ice dispersal	5% of 3-5 y subadults	Expert opinion (tested range of 0% to 10%)	Unknown
Intrinsic population growth (r)	0.059	Calculated from mean demographic rates	

Field = estimate based on reports of field studies. Intrinsic population growth rate (r) based on estimated demographic rates in the absence of climate change. See Methods text for further explanation and references.

the estimated predation by polar bears, the remaining non-bear mortality rates for the bearded seal model were 7.1%, 2.9%, 2.9%, and 0.1% in the first year, 2nd, 3rd, and later years, respectively. Our estimates project that most of the bearded seal mortality can be accounted for by predation by polar bears, therefore, we may have underestimated total mortality or overestimated the proportion killed by bears. The carrying capacity (K) was set at 125% of the initial population size to allow for some population expansion.

Key demographic parameters for the bearded seal population are summarized in Table 2. Complete listing of the values entered into the Vortex population model are provided in the annotated input in Supplementary Material.

2.1.3 Polar bear population and demography

The size of the Barents Sea subpopulation of polar bears was estimated to be N = 2,650 in 2004 (Aars et al., 2009), out of a total circumpolar Arctic estimate of approximately 26,000 for the 20 recognized populations combined (Regehr et al., 2016; Laidre et al., 2022). The Barents Sea subpopulation was heavily harvested until 1973 (with an average of 320 bears taken per year from 1945-1970; Derocher, 2005) but has grown in the subsequent decades following protective legislation and is likely still recovering (Aars et al., 2017).

Polar bears in Svalbard usually produce their first litter when females are 6 y (mating at age 5 y) of age or older, although they occasionally have cubs at when they are 5 y (Derocher, 2005). We set the initial age of breeding in the models to be 6 y. Females will not produce a subsequent litter while they still have dependent cubs. Females that successfully wean litters can produce their next litter after a 3-year inter-birth interval. If all cubs in a litter die before weaning, females can breed that year to produce a litter the next year (if the prior litter dies early enough in the year for mating to take place in late spring). The individual-based simulation tracked when females produced cubs and when those cubs died to determine at each year if a female had dependent cubs. If a female lost a litter from one of the prior two years, we specified in the model that she would have a 25% probability of being able to recycle and mate again that year. Otherwise, she could not mate again until the following year.

Of the adult females that are available for mating, we specified that 90% (± 5% environmental variation, EV) produce a litter. Given the restriction on breeding by females with dependent cubs, this leads to a mean of 40% of adult females producing a litter each year in our model, which is similar to the values of 37.5% reported by Derocher (2005) and 41% reported by Wiig (1998). We specified the distribution of litter sizes to be 31% a single cub, 66% twins, and 3% triplets, resulting in the reported mean of 1.72 (Derocher, 2005). We assumed that the sex ratio of newborns is 1:1. We specified in the model that dependent cubs will die if their mother dies.

Males in Svalbard have been seen with females during the mating season from the age of 4 y, but scarring, fresh wounds, and age distribution among males having access to females, suggests that 6 y is a typical age for males to start to reproduce. Derocher et al. (2010) showed that few young adult males were seen with females in mating pairs. However, Zeyl et al. (2009) showed from genetics that young males were more successful than suggested by observations. Based on this combined information, we assumed that

TABLE 2 Key demographic parameters used to model bearded seal population in the northern Barents Sea.

Parameter	Estimate	Source	Predicted effects of climate change
1st age of female reproduction	6	Field	
1st age of male reproduction	7	Field	
Oldest reproduction	25	Field	
Litter size	1	Field	
% adult females producing pups	90%	Expert opinion	
Maximum age	25	Calculated from mortality rates	
Pup mortality	25%	Calculated to fit population growth rate	Could decrease if abundance of polar bears declines, or could increase if polar bears switch from preying on ringed seals to preying on more bearded seals.
Subadult annual mortality	10%	Calculated to fit population growth rate	Could increase if abundance of polar bears declines, or could decrease if polar bears switch from preying on ringed seals to preying on more bearded seals.
Adult annual mortality	10%	Calculated to fit population growth rate	Could increase if abundance of polar bears declines, or could decrease if polar bears switch from preying on ringed seals to preying on more bearded seals.
Current population size (in study region of Barents Sea)	50,000	Expert opinion	
Maximum population size	62,500	Estimate to allow for some growth	
Intrinsic population growth rate (r)	0.048	Calculated from mean demographic rates	

young sexually mature males (6-10 y) are 80% as likely as older males to breed in our models.

Mortality rates for polar bears in Svalbard have been estimated for adult females based on data from satellite telemetry collars (Wiig, 1998), and for animals of different ages based on capture/recapture data (Cubaynes et al., 2021). Litter production rates have been reported both in Cubaynes et al. (2021), and in Naciri et al. (2022), where the latter study showed an increase in production with age for females, increasing from young ages up to prime age females, followed by a sharp decrease with old age. The values presented below are based on these sources. First year mortality of cubs was set at 85% for primiparous females and 50% (EV of ± 10% SD) when the mother had experience with at least one prior litter. The annual mortality of dependent cubs in each of the next two years was set to 20% (± 5% SD). Annual mortality from 3 y to physical maturity at 6 y was set to 3% (± 1% SD). For adults, annual mortality was set to 2% (± 1 SD) up to 18 y, 10% from 18 y to 22 y, and 20% after 22 y. Maximum longevity was set to 28 y, and breeding occurred only up through 25 y of age, so that females would be able to survive to rear their last litter to independence. These values generate a maximum population growth rate of 2.1%.

The carrying capacity (K) was modeled as an upper limit on the number of independent bears (3 y and older). When K was exceeded, additional mortality with a probability of (N-K)/N was applied to each individual across all age classes to bring the population size back down to K. Based on harvest levels, the historic population size across the region was likely 6,000 or more, although some of that would have been from Greenland (i.e., outside of the area we are modeling). It is not known if the current carrying capacity is as large as it was for the historic population, because sea ice habitat has declined markedly over the last three decades in the area (Stern and Laidre, 2016; Urbanski and Litwicka, 2022). We can estimate the number of bears that could be supported by the prey base of bearded seals, ringed seals, and other prey – using the energetic calculations described below (also see Stirling and Øritsland, 1995). With the estimates of predator-prey relationships in our metamodel, we observed that predation by the polar bear population on bearded and ringed seals is unsustainable (driving the seal populations down and consequently causing collapse also of the bear population) if the bear population grows to a size such that it takes more than 15% of the combined prey populations each year. Thus, we can define the carrying capacity of the polar bear population as being the size that can be supported by a predation rate of 15% per year (i.e., K = 0.15 x available biomass of ringed seals, bearded seals, and other prey/43.5 required prey per bear [see below]). With the seal populations able to grow to an estimated 125% of current sizes (see above), this leads to an upper limit of K for the population of 3605 independent polar bears, or 4532 total bears including cubs still dependent on their mothers.

Key demographic parameters for the polar bear population are summarized in Table 3. Complete listing of the values entered into the Vortex population model are provided in the annotated input in Supplementary Material.

2.1.4 Interactions between the species

Figure 1 illustrates linkages between the species that we considered within the metamodel. Increases in stocks of prey increase the total prey available to polar bears and thereby increases the carrying capacity for bears (K-adults) but decreases the relative predation (having a positive impact) on each prey type because that prey becomes proportionately less of the prey base for the bears. An increase in the bear population increases predation on all of the prey species (although "other" prey in our model is assumed to be a constant, being a range of individually minor prey species that are not themselves strongly affect by polar bear predation). The number of bear cubs that can be reared (K-cubs) is positively related to the number of ringed seals on the land-fast sea ice, while the number of ringed seal pups that can be raised on the land-fast sea ice (K-pups) is dependent on the springtime ice and snow cover (Kovacs et al., 2024). The numbers of ringed seals in each of the two subpopulations receives augmentation from immigrants dispersing from the other population (but in turn is reduced by the number of emigrants). Ice cover around the archipelagos is modeled as a direct effect only on the number of ringed seal pups that can be raised on the land-fast sea ice but has indirect impacts on other parts of the system through the various interdependencies.

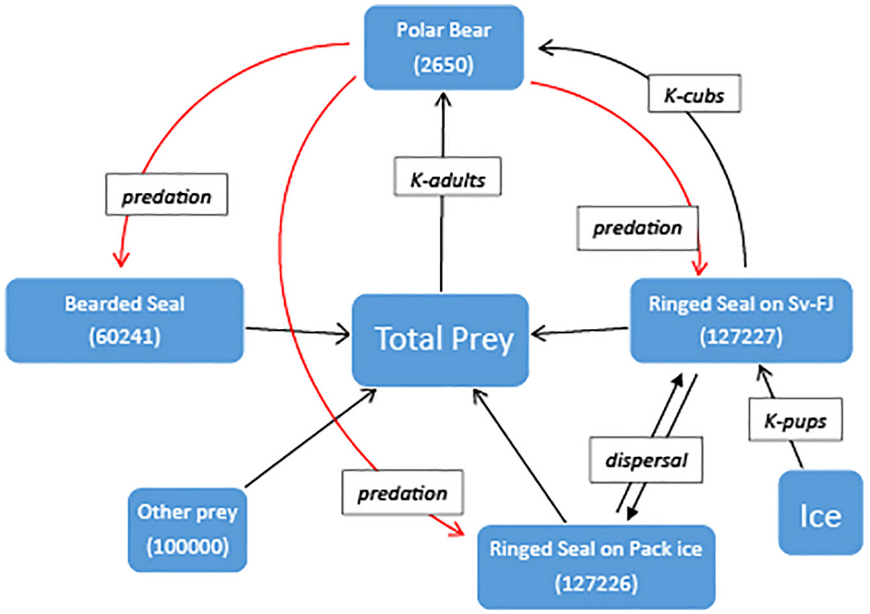
To model how the effects of changing sea ice conditions cascade through this predator-prey system, we specified quantitative relationships that describe ways in which the species impact each other and how each species and their interactions depend on the ice. The amount of predation by polar bears on the prey species was estimated from energetic calculations of the prey availability, food value, and energy requirements of the bears. The total available prey to support the polar bear population was estimated by assuming that the prey base is comprised of the ringed seals (the primary prey), bearded seals (less abundant prey), and all other prey (harp seals (*Pagophilus groenlandicus*) and other seals (including walruses *Odobenus rosmarus*), bird eggs (Prop et al., 2015), reindeer (*Rangifer tarandus platyrhynchus*; Stempniewicz et al., 2021), and whale carcasses (Aars et al., 2015; Laidre et al., 2018)). Mature ringed seals are 50-100 kg (Kovacs et al., 2021b); while an adult bearded seal is about 250 kg (Andersen et al., 1999). However, bears prey on young seals more heavily than adults. At birth, ringed seals average 4.5 kg, and they grow to 20 kg by the time of weaning at six weeks of age (Lydersen and Kovacs, 1999). Bearded seals average 38 kg at birth, and they grow rapidly to 80-120 kg when weaned at three weeks of age (Kovacs et al., 2020). Without knowing precise proportions of seals preyed upon at each age for each species, we cannot determine the relative energy value of an average ringed seal vs bearded seal eaten. However, based on average sizes of the two species, we assumed that the average bearded seal taken by a polar bear is 8 times larger than the average ringed seal that is taken. We also tested some scenarios with a 5:1 ratio of energy value of bearded to ringed seals (see Sensitivity analyses, below).

Other prey species are individually much less abundant in the diet of polar bears and typically provide much less energy to bears. However, collectively and over the entire year they might provide an amount of food equivalent to that which the bears derive from predation on ringed seals. For the model, it was assumed that these other food sources would remain stable through the model run time frames.

Reports of polar bear diets suggest that proportions of various prey species vary by location, season, and for individual bears. Derocher et al. (2002) reported a distribution of 63% ringed seal, 13% bearded seal, 8% harp seal, and 16% unknown species (with a biomass distribution of 30% ringed, 55% bearded, and 15% harp seals) in the diet of polar bears in Svalbard and the Barents Sea. Iversen et al. (2013) reported that polar bear scats in Svalbard contained mostly ringed seal pups, but bearded seals might be a

TABLE 3 Key demographic parameters used to model polar bear population in the northern Barents Sea.

Parameter	Estimate	Source	Predicted effects of climate change
1st age of female reproduction	6	Field	
1st age of male reproduction	6	Field	
Oldest reproduction	25	Field	
% adult females producing pups	90% of females without dependent cubs	Field	
Litter size	31% of 1, 66% of 2, 3% of 3	Field	
Maximum age	28	Field	
Cub mortality	85% for primiparous females; 50% for experienced females	Field	Increased if less prey available on land-fast ice
Subadult annual mortality	20% while dependent on dam; 3% up to breeding age	Field	
Adult annual mortality	2% up to 18 y, 10% from 18 y to 22 y, and 20% after 22 y	Field	
Current population size (independent bears)	2650	Field	
Maximum population size (independent bears)	Function of prey abundance; 3605 when seals at maximum	Calculated	Decreased if key prey base (ringed seal pups) on land-fast ice decrease
Intrinsic population growth (r)	0.021	Calculated from mean demographic rates	



Total prey
= RSeals + BSrse * BSeals + OtherRSE
Total prey, weighted by bear preference (pRSE)
= pRS * RSeals + pBS * BSrse * BSeals + pOther * OtherRSE
Predation on ringed seals
= BigBears * Need * pRS * RSeals / pRSE
Predation on bearded seals
= BigBears * Need * pBS * BSeals / pRSE
Ice-limited number of ringed seal pups on Sv-FJ (*K-pups*)
= MaxPups * pSvFJ * (1 - Y * rate of ice decline)
Carrying capacity for polar bear cubs (*K-cubs*)
= Sustainable removal * proportion of prey taken by adult females * SvFJpups / cubCost
Carrying capacity for adult polar bears (*K-adults*)
= Sustainable removal * pRSE / Need

FIGURE 1
Linkages between components of this predator-prey system considered within the metamodel. Starting values for each population are given in parentheses. Black and red arrows representing positive and negative relationships, respectively. Italicized text boxes note the mechanisms through which the relationships act, according to equations given below, with parameters "OtherRSE" – other prey, scaled as "ringed seal equivalents" of energy value; "BSrse" – energetic value of a bearded seal relative to a ringed seal; "pRS", "pBS", and "pOther" – proportional predation by polar bears, relative to abundance of prey species; "BigBears" – Polar bears independent from dam; "Need" – Polar bear energetic need (43.5 RSE/y); "MaxPups" – number of ringed seal pups produced when seal population is at carrying capacity; "pSvFJ" – proportion of ringed seals on Svalbard-Franz Josef; "SvFJpups" – number of ringed seal pups on Svalbard-Franz Josef; "cubCost" – Energy required to raise a cub (7.35 RSE).

much larger part of the diet of polar bears feeding offshore (not sampled in that study). We assumed that polar bears prey on ringed seals, bearded seals, and other prey in proportion to their availability. Because bearded seals (at the ages taken by polar bears) are larger than ringed seals, but about 25% as abundant, this means that polar bears would take ringed seals about 4x as often as bearded seals, but the polar bear diet would consist of twice as much biomass of bearded seals compared to ringed seals. With estimated current abundances of adults and annual production of pups, the dietary biomass distribution at the outset of our simulation would be 30% ringed seal, 58% bearded seal, and 12% other prey, closely corresponding to the estimates of Derocher et al. (2002). If we estimate a lower relative energy value for bearded seals (e.g., 5-fold more than ringed seals), the proportion of each prey in the diet would remain the same, but more of each prey species would need to be consumed to meet the energetic needs of the bears, and the distribution of biomass would shift (e.g., to 39%, 46%, 15%). We also tested a few models in which we specified a greater preference for ringed seals (see Sensitivity analyses, below), which shifts both the numeric distribution and biomass distribution of prey consumed.

In order to determine how many polar bears (K) can be supported by the prey base, and how many ringed seals and other prey species are killed annually by the bears, it is necessary to estimate the energetic requirements of the polar bear population. The energy needs for an "average bear" (range 5-500 kg, young, subadults, adult females and adult males) per year was approximated based on a simplification of Stirling and Øritsland

(1995) calculations, using a mass of circa 200 kg. The basal metabolic rate (BMR) estimated according to Kleiber (1975) is 70 x BM^0.75 = 3.72 Mcal/day (15.6 MJ/day). The field metabolic rate (FMR) of free-living animals is generally somewhere between 2-4 times the BMR (Nagy, 1987). Polar bears are able to conserve energy in periods with little food by lowering their metabolic rate, and FMR was thus set to 2 x BMR. (See Stirling and Øritsland (1995) for discussion of this topic). Thus, the annual energy requirement for the average polar bear would be 3.72 Mcal/day x 2 x 365 = 2 715.6 Mcal/year (11 362 MJ/y). According to Stirling and Øritsland (1995) an adult ringed seal provides about 150 000 kcal of energy for a polar bear, subadults provide about 50 000 kcal, and pups provide about 10 000 kcal for the first two weeks after birth, 50 000 kcal for the next two weeks, and about 100 000 kcal thereafter. If the proportion of kills are 50% pups under two weeks of age, 30% 2-4 weeks, and 20% older, then the average ringed seal pup provides about 40 000 kcal to a bear. Polar bear predation on ringed seals was estimated to be about 56% on pups, 26% on 1-2 y subadults, and 18% on adult-size seals by Stirling and Øritsland (1995). Therefore, the average ringed seal killed provides 62 400 kcal (261 MJ), and a bear needs to kill 43.5 such "ringed seal units" to meet its annual energy requirements. Adult male polar bears weigh about twice as much as females, but without dependent cubs - males might travel farther in search of prey. If our calculations underestimate the average energy requirements for adult bears, we might be overestimating the number of bears that can be supported by the prey base. If so, the upper limit on the number of polar bears projected in the early years of our models (before there is significant loss of sea-ice) would be less, and the subsequent decline in polar bears as ringed seal populations on the archipelago decline would be accelerated. The metamodel parameters defining the predator-prey linkages are summarized in Table 4.

In each year of the simulation, the total prey consumed by bears was calculated from the number of independent bears and the energy requirements per bear, and this predation was allocated among the three types of prey based on the relative availability of their biomass. Predation was further allocated among the age classes of ringed seals and bearded seals. For ringed seals, bear predation has been reported (Stirling and Øritsland, 1995) as 56% on pups, 26% on 1–2-year-olds, and 18% on adults. For bearded seals, lacking field data, we assumed that predation is distributed as 30% on pups, 15% on 1–2-year-olds, and 55% on adults, because bearded seal pups are able to escape predation at an earlier age than are ringed seals.

The critical dependency of female polar bears with cubs-of-the-year on the availability of ringed seals in the breeding areas on the land-fast sea ice around the archipelagos when the bears emerge from the den was modeled by assuming that the number of bear cubs that can be raised each year is limited by the availability of ringed seals on the land-fast sea ice at this time of the year. We assumed that 50% of the ringed seal pups were accessible to bears. If this proportion was not taken, polar bear cub survival declined because of the lower prey capture rate. Other values for this limiting of the harvest rate were tested during sensitivity analyses (see below). The ringed seal population model (with the parameter values given above) estimates that currently 29% of ringed seal pups are killed by bears. We also assumed that half of the predation on ringed seals would be by bears other than females with cubs. To raise cubs, a female bear needs to kill on average 12.5 ringed seals, which is 7.35 ringed seals per bear cub (with a mean litter size of 1.7). We therefore set the number of bear cubs that could be raised each year to be no more than the number of ringed seal pups in Svalbard and Franz Josef Land x maximum proportion harvested (0.5) x proportion killed by females with cubs (0.5), divided by the requirement for 7.35 seals/bear cub. Female polar bears that are raising cubs prey on all ringed seal age classes, but we assume that without the available ringed seal pups in breeding areas, the bears could not get enough high energy food when they emerge from dens in the spring to be able to successfully raise their cubs. Thus, survival of polar bear cubs can be estimated as a function of the abundance of ringed seal pups on the land-fast sea ice. At the outset of the simulation, this equates to a maximum of 926 cubs that female bears can raise in Svalbard and Franz Josef Land. Given the age structure and reproductive rates described above, the current

TABLE 4 Metamodel parameters defining predator-prey linkages, with best estimates as used in Baseline model and ranges evaluated in sensitivity analyses.

Parameter	Baseline		Sensitivity analysis	
	Estimate	Source	Low value	High value
Decline of land-fast ice	1%/y	Conservative projection	1%/y	10%/y
Energetic requirements of polar bear	2,715.6 Mcal/year	Calculated		
Mean energy available per ringed seal prey	62,400 kcal	Calculated		
Energy value of bearded seal prey relative to ringed seal	8	Calculated	5	8
Abundance of bearded seals relative to ringed seals	0.25	Expert opinion		
Polar bear preference relative for bearded seals relative to ringed seals	1.0	Expert opinion	0.5	1.0
Proportion of ringed seal pups accessible to polar bears	0.5	Expert opinion	0.25	1.00
Availability of prey other than ringed seals and bearded seals, scaled as "ringed seal equivalents" of energetic value	100,000	Expert opinion		

bear population would be producing an estimated 609 cubs per year, indicating that in our model the availability of ringed seal pups is not currently a limiting factor restricting the number of bear cubs surviving. The limitation on the number of bear cubs if the ringed seal population declines in the future was modeled by specifying that when the maximum number of cubs for a year was exceeded by births, then cub survival was decreased proportionately to the excess of cubs born.

In models projecting sea ice cover over time, it was assumed that reduced pupping habitat for ringed seals in Svalbard and Franz Josef Land reduces the number of ringed seals pups available to mother bears emerging from their dens with cubs. It was assumed that the reduction in ice cover has no impact on the subpopulation of ringed seals that gives birth on the pack ice (at this point in time). In addition, it was assumed that the total carrying capacity for adult ringed seals was not diminished by the loss of ice.

Although the decline in the ringed seal subpopulations that pup on the fjord ice of Svalbard or Franz Josef Land could perhaps have been modeled as a direct consequence of polar bears being able to prey on more of the pups if they become more densely packed under reduced sea ice conditions, rather than being projected to decline linearly with ice cover, other species such as arctic foxes (*Vulpes lagopus*) and glaucous gulls (*Larus hyperboreus*) also exploit the easy availability of ringed seal pups when ice and snow conditions do not provide an opportunity for ringed seals to create lairs on the ice to protect the pups (Lydersen and Smith, 1989). Without knowing the details of the feeding behaviors and abundances of these other predators, mechanistic models of the causes of decline for ringed seals are not possible; the critical dependency of ringed seals on the ice for reproduction was thus modelled simply with the local carrying capacity being linearly related to the ice cover available for raising pups.

2.1.5 Projections of changing ice cover

Seasonal minima and maxima projected for large regions from global climate models provide the most robust predictions of average changes to Arctic climate (IPCC, 2023). However, for the polar bear – ringed seal relationships around Svalbard, what matters is the extent of land-fast sea ice cover in April (when seals have pups and polar bears have emerged from dens with cubs), and the snow cover that has accumulated on that ice (Hezel et al., 2012). Sea ice on the Barents Sea in April declined by about 13.4% per decade from 1979 to 2021 (Isaksen et al., 2022) and Hezel et al. (2012) project a 70% decline in snow-covered ice adequate for ringed seal lairs by 2100. We therefore initially tested the impact of a conservative, linear 1% annual decline in the springtime land-fast sea ice in our models. However, documented increases in the rate of change of Arctic sea ice, along with increasing water temperatures led us to explore faster rates of decline as well, projecting impacts of sea ice declines up to 10% per year (i.e., complete loss of sea ice over the next decade.

2.1.6 Metamodeling approach

The three PVA models were created in the Vortex software, and we examined the projections for each species to verify that population growth rates and age structures were consistent with the species biology when initial baseline values for the abundances of the other species were entered as fixed parameters. The three PVAs were then linked into a metamodel via the MetaModel Manager software (Lacy et al., 2013; Pollak and Lacy, 2020; program and source code available at https://scti.tools/metamodelmanager). The functional relationships connecting the species were specified in the three Vortex PVA models via state variables that track changing parameters (such as prey abundances) and derived variables (such as the maximum number of cubs that can be raised), which are in turn used in functions that specify demographic rates (such as cub survival). The current value of each state variable during the simulation was shared among the three PVA models via the MetaModel Manager program, with specification that in each year of the simulation control would cycle among the PVA models in the sequence ringed seal, bearded seal, and then polar bear. For example, in each year of the simulation, the ringed seal PVA model would set a state variable for the number of pups born on the land-fast sea ice, and this variable would be passed to the other PVA models so that it could be used as a determinant of bear cub survival that year. In data flow back to the seal PVA models, the bear PVA would set a state variable calculating the number of independent bears each year, and that variable would then be used in the ringed seal and bearded seal PVAs to determine the number of each species killed by the bears.

Sensitivity analyses were run to explore plausible alternative parameters describing the interactions among the species, including: higher or lower rates of movement of ringed seals between breeding on the land-fast sea ice and the pack ice; greater preference of polar bears for ringed seals; reduced average food value of bearded seals; changed proportion of ringed seal pups available to the bears; and annual rates of decline of land-fast sea ice from 1% to 10%.

Each scenario was simulated for 100 years, and simulations were each repeated 100 times to obtain estimates of means and SD for the population size over time. All input files for the three Vortex models and MetaModel Manager are available on the Zenodo repository at DOI 10.5281/zenodo.11265382. Notes included in the Vortex input files and provided in the Supplementary Material provide further explanations of model structure and parameter estimates.

3 Results

3.1 Baseline model

In the absence of any changes to the springtime ice cover, the metamodel generates predator-prey dynamics that are consistent with the existing populations and their recent trajectories (Figure 2). The seal populations are able to support the polar bear population. Within 5 to 6 years, the ringed seals and bearded seal populations grow to their carrying capacities, set at 125% of the initial population sizes, with growth rates in the first few years of 4.3% and 4.7%, respectively. After a small initial decline while the metamodel dynamics modified the starting age structure, the

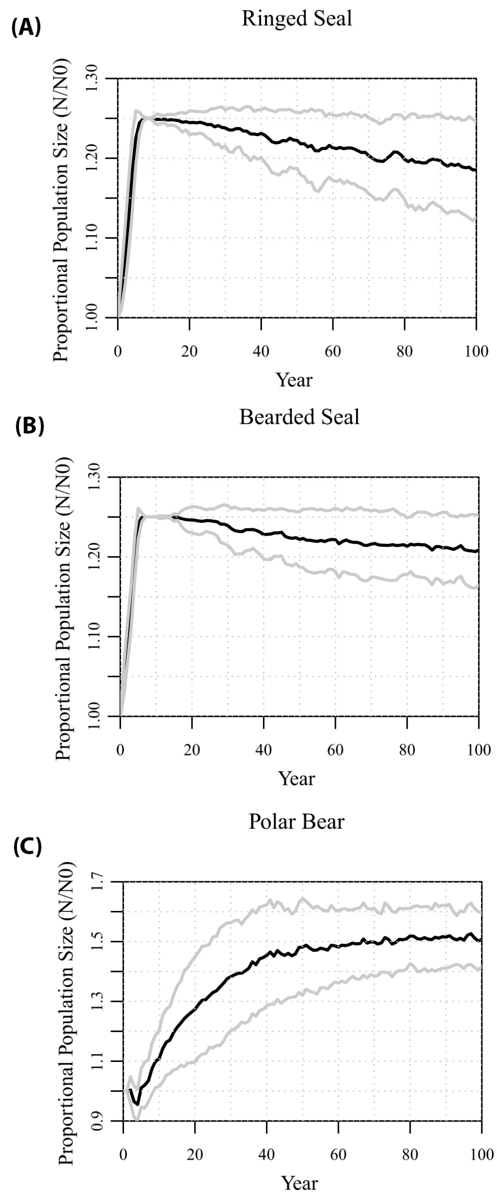


FIGURE 2
Projections of population sizes relative to starting numbers of **(A)** ringed seals, **(B)** bearded seals, and **(C)** polar bears from 100 iterations – with an assumption of no decline in land-fast sea ice. Gray lines show variation across iterations as ± 1 SD.

polar bear population was also projected to grow, although at a slower rate (about 1.3%) than the prey populations. After about 20 years, the bear population had increased by about 30%, and the seal populations consequently began to decline slightly. After about 50 years, all three species stabilized at numbers above the starting sizes, with prey populations about 18% to 21% above initial sizes, and the polar bear population about 50% above its initial size. The projections showed fluctuations around these predator-prey dynamics, with predicted sizes that varied with a SD across independent iterations of about ± 10% of the means.

3.2 Sensitivity analyses of metamodel parameters in the absence of climate change

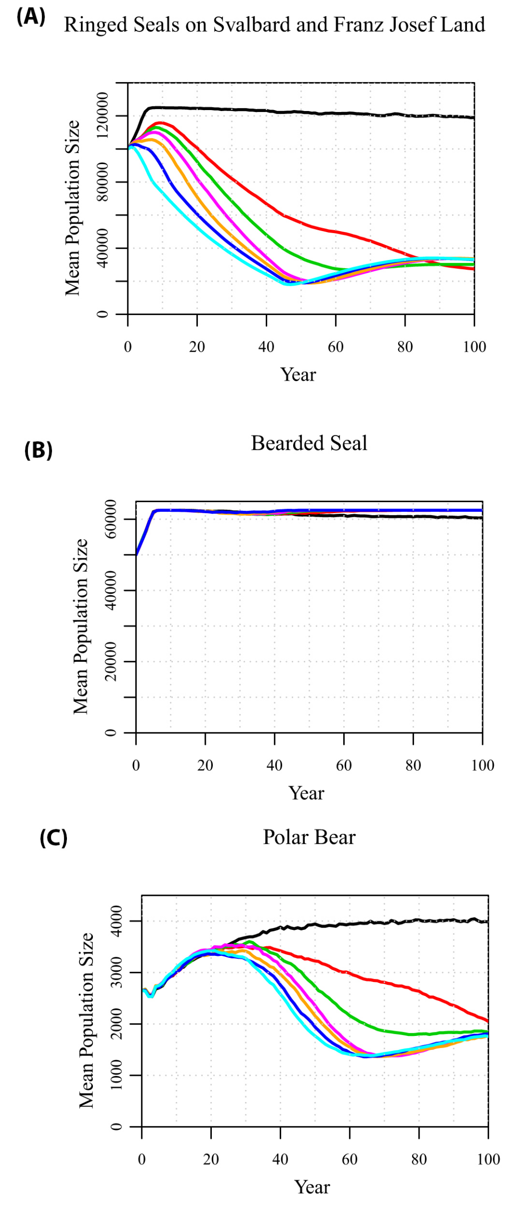
Alternative values for a number of the uncertain model parameters, which describe the linkages between the species, were tested. Scenarios with either 0% or 10% annual dispersal of subadult ringed seals between the population breeding on the land-fast sea ice and the population on pack ice generated mean trajectories that were virtually indistinguishable from the baseline metamodel above (results not shown). This occurred because in the absence of a decline in ice cover, the population of ringed seals on the land-fast sea ice grows to, and remains near, carrying capacity even with increasing polar bear predation (see above).

If polar bears are assumed to prey preferentially on ringed seals, relative to their abundance, then the predator-prey dynamics would be projected to be unstable, with ringed seals unable to sustain the initial predation rates, and polar bears subsequently also declining after the prey base is diminished (the lines showing shallower or steeper declines for scenarios “BS preference = 0.75” and “BS preference = 0.50”, respectively, in Supplementary Figures S1A, S1C). This suggests that scenarios with a reduced preference (or ability) by polar bears to prey on bearded seals relative to ringed seals are not good representations of the system, because ringed seals, bearded seals, and polar bears do currently co-exist in the Barents Sea. Other parameter values examined in the sensitivity analyses all resulted in stable predator-prey dynamics after initial growth phases, although the initial growth of the bearded seal population was slower when they provide less energy value to the bears, as a consequence of the bears taking more seals to meet their energy needs (see Supplementary Figure S2B), and the final population size of the bears was less if they could effectively access a smaller percent of the ringed seal pups or if bearded seals provided less energy (Supplementary Figures S2C, S3C). Small differences among scenarios in the final population sizes of the seals were as expected: both prey species remain closer to their carrying capacities in the two scenarios in which polar bears are less abundant because of more limited availability of prey (“BS = 5 RSE”, Supplementary Figure S2; “25% RS pups accessible” Supplementary Figure S3). There was moderate variation among the independent iterations for those scenarios in which the populations did not remain near their carrying capacities (see 90% confidence intervals in Supplementary Figures S1–S3), but the baseline model showed stable population sizes with minimal variation across iterations. These sensitivity analyses verify that the baseline model provides a reasonable scenario that represents the predator-prey dynamics better than models with some plausible alternative estimates of the species interactions.

3.3 Population projections in scenarios with declining ice cover

With a conservative, projected 1% annual decline in land-fast sea ice in April, the ringed seal population in Svalbard and Franz

Josef Land initially starts to grow but after a decade enters a decline (Figure 3A). Consequently, the polar bear population is projected to start to decline from its peak size after about three decades (Figure 3C). The decline in the bear population lags behind the decline in ringed seals by a few decades, because the impact of declining ice is on ringed seal recruitment rather than on adult survival, and the subsequent impact of declining ringed seal pups is on bear recruitment. In the decades around the peak bear numbers, the ringed seals on the pack ice (not shown) and the bearded seals (Figure 3B) show small temporary declines, as a result of the still high levels of bear predation. After the polar bears begin to decline, then the bearded seals recover and remain near carrying capacity.


(A) Ringed Seals on Svalbard and Franz Josef Land

(B) Bearded Seal

(C) Polar Bear

FIGURE 3
Projections of population sizes of **(A)** ringed seals in Svalbard and Franz Josef Land, **(B)** bearded seals, and **(C)** polar bears, when there is a 0%, 1%, 1.5%, 2%, 3%, 5%, or 10% annual decline (from top to bottom) in the springtime land-fast sea ice.

If sea ice cover declines are more similar to current expectations, occurring at rates of 1.5% to 3% per year, the decline in ringed seals, followed by decline in polar bears, occurs more quickly and to a greater extent. After 50 to 60 years, by which time there would be little or no spring land-fast sea ice around the archipelagos, the ringed seal population around Svalbard and Franz Josef Land hits a minimum at about 20% of its initial size. The polar bear population hits its minimum about a decade later, and this allows the ringed seal population to recover slightly. This remnant population of ringed seals persists because the initial model assumes that each year 5% of subadult ringed seals from the pack ice subpopulation move down to Svalbard or Franz Josef Land. Thus, the pack ice subpopulation of ringed seals remains near carrying capacity, while the steady flow of ringed seals moving down to the archipelagos provide an ongoing (although much reduced) annual production of ringed seal pups, which provides food for polar bears emerging from dens with cubs. Even higher rates of ice loss, 5% to 10% per decade (i.e., complete loss of land-fast sea ice on the fjords in 20 or 10 years), lead to only marginally faster declines in ringed seals (Figure 3A) and polar bears (Figure 3C), due to the assumed immigration from the pack ice population of ringed seals sustaining a remnant population of polar bears.

As springtime ice cover on the fjords of the archipelagos diminishes, it would become maladaptive for ringed seals to move from the pack ice into the declining population near the coast, where they have no prospect of experiencing conditions necessary to rear pups. If there is no dispersal of ringed seals from the pack ice to Svalbard and Franz Josef Land, then the decline of ringed seals on the land-fast sea ice and of the polar bears that depend on them accelerates (Supplementary Figure S4). At higher rates of loss of spring sea ice (e.g., 2 to 3% per year), the ringed seal population breeding around the archipelagos disappears after 55 to 65 years if it is not continually replenished from the population breeding on the pack ice, and extirpation of the polar bear population denning and breeding on the archipelagos follows about 20 years later.

To explore further the sensitivity of the collapse of the seal and bear populations to immigration of ringed seals from the pack ice, Supplementary Figure S5 compares mean population trajectories for the scenarios with a 2% annual decline in sea ice cover and dispersal of subadult seals between the pack ice and the archipelagos at annual rates varying from 0% to 5%. Even a low rate of movement of pack ice seals into the archipelagos to attempt to breed there (although without any success after the spring land-fast sea ice cover is completely gone) is projected to sustain a small breeding population of polar bears. However, this projection is dependent on the assumptions that the alternative prey base will continue to be sufficient to support the adult bears.

4 Discussion

Ringed seals are key prey for polar bears and human inhabitants in coastal Arctic communities across the circumpolar Arctic. Their range extends further north than most other seals because they can maintain breathing holes through quite thick sea ice. However, they are dependent on quite specific ice and snow conditions in the spring in order to construct snow lairs in which they rear their pups. They are therefore highly vulnerable to the ongoing declines in sea ice in the Arctic (Laidre et al., 2008; Kovacs et al., 2011, 2012, 2021a, 2024; Reimer et al., 2019). Bearded seals are another important Arctic seal species throughout the circumpolar Arctic, that is a favored hunting target for some Alaskan communities and a significant contributor to polar bear diets (Derocher et al., 2002; Nelson et al., 2019). Bearded seal pups are large at birth, and swim within the first hours of life, making them somewhat less accessible to polar bears than ringed seal pups (Lydersen et al., 1994; Lydersen and Kovacs, 1999; Kovacs et al., 2020), and adults spend relatively little time hauled out, reducing their availability to polar bears somewhat (Hamilton et al., 2017). Because bearded seals forage on a wide variety of prey species, will more readily haul out on land, and have pups large enough to use glacier ice pieces (or potentially land), they might have more climate resilience than ringed seals, though they are still likely to be negatively impacted by global warming (Kovacs et al., 2020). There are few data available to examine the changes that are occurring in population trends for these seals species, so we have used modelling forecasts herein, combined with similar projections to follow their principal predator, the polar bear in the Barents Region.

Female polar bears are dependent on finding high calorie, easily accessible prey quickly after den emergence in order to recover fat reserves lost during the fasting period in the den and to fuel increased milk production for the active, growing cubs when they shift out of the den (Archer et al., 2023). Females with cubs of the year are not free to swim in open-water or loose ice areas, so not surprisingly they focus their hunting effort in areas with land-fast sea ice where ringed seals lairs are most dense, such as at glacier fronts in Svalbard (Freitas et al., 2012; Lydersen et al., 2014). Alternative prey, such as bearded seals, probably cannot fill the critical energetic needs in the early spring when females have very young cubs. Spring feeding on ringed seals is also important to other polar bears (males and juveniles) that acquire most of their annual energy intake at this time (Stirling and Øritsland, 1995). Later in the season other prey can be utilized (Hamilton et al., 2017), although the energetic values of birds, reindeer and other terrestrial prey is unlikely to fully compensate for the loss of ice-seals from the polar bear's diet (Whiteman et al., 2017; Hunter et al., 2010; Pagano et al., 2024).

In this study we used multiple Population Viability Analysis models linked into a metamodel to examine the inter-dependencies of ringed seals, bearded seals, and polar bears in the Barents Region and to project potential impact scenarios of changing sea ice on this predator-prey system. To build these models, estimates of detailed demographic parameters on each species were required in addition to understanding the constraints on how the species interact, data on the energetic values of prey and requirements of the predator, and projections of changing sea ice conditions. Data are not available to provide accurate estimates for all of the demographic rates needed for these three arctic species, so informed estimates were often used as inputs to our models. Moreover, the impacts of changing climate on these species will almost certainly include additional processes/stressors that we have not modeled. Even so, the dynamics revealed in the metamodel of a predator-prey system in which the relationships among species are strongly determined by the sea ice conditions in the Arctic likely do represent reasonable approximations of the impacts that can be expected. The projected trends indicate that currently abundant species are likely to be highly vulnerable to effects of climate change and experience significant declines. Our metamodel also provides a framework for including new data into future projections of climate change impacts as they become available.

The most dramatic and easily intuited prediction from our metamodel is that as the sea ice conditions that allow ringed seals to raise pups in snow-covered lairs on the frozen fjords of Svalbard and Franz Josef Land decline or even disappear (see Kim et al., 2023) our marine mammal populations will be negatively impacted. Ringed seal populations will collapse due to lack of successful recruitment. Consequently, the polar bear populations that depend on ringed seal pups to be able to raise their own offspring are likely to follow similar trends. Dispersal of ringed seals from the pack ice might slow extirpation of coastal subpopulations, with the ringed seals that use land-fast sea ice becoming demographic sinks rather than the strongholds for the species that they have been in the past. Interestingly, our models suggest that the populations of ringed seals using drift ice, and bearded seals, are projected to maintain slightly larger population sizes in the long-term, because the decline in the regional population of polar bears reduces predation pressure. However, our models do not reflect the on-going reductions in drift ice, which we fixed as a constant, although this ice has become thinner, more fractionated, more mobile, and less extensive (Isaksen et al., 2022). In the coming decades remaining sea ice in the Arctic will largely occur over deeper, off-shelf waters. Although there are signals of increasing primary production in the Arctic Ocean, the deep ocean is less productive than the Arctic shelf seas (Ardyna and Arrigo, 2020).

Although the directions of change to the populations modeled herein have been predicted for some time (e.g. Tynan and DeMaster, 1997; Laidre et al., 2008; Durner et al., 2009; Stirling and Derocher, 2012) the dramatic magnitudes of the estimated changes are perhaps surprising. Our estimated timeline is almost certainly overly optimistic given that the rate of sea ice decline has accelerated over recent years in the Barents Region and drift ice, similar to land-fast sea ice, has declined markedly (Isaksen et al., 2022; Urbanski and Litwicka, 2022). Land-fast sea ice coverage in open fjords in western Svalbard collapsed in 2006 and has not recovered since; sill fjords still retain more ice, but there are fewer tide-water glaciers calving pieces onto the annual ice and less precipitation in winter comes as snow (there is more rain) so there are fewer drifts even on available ice. The predicted declines in ringed seals and bearded seals will almost certainly lead to a collapse of polar bears in the Barents Sea area. At very least the remaining polar bear population will be smaller than current numbers (Aars et al., 2009, 2017) despite the various foraging and distributional plasticity being shown currently by the polar bears in the region (Prop et al., 2015; Hamilton et al., 2017; Bengtsson et al., 2021; Stempniewicz et al., 2021).

Our metamodel also shows that with long-lived species, impacts that reduce reproductive success, even to almost zero, might not be easily observable from census data on adults until a decade or more after climate changes have in fact disrupted the community. Field monitoring of demographic changes combined with models that project the consequent population dynamics will be required to reveal the full scope of the consequences of climate change impacts that are already underway. Our models project an initial rise in both predator and prey populations, for about a decade, as a consequence of reduced hunting compared to the historical situation. The subsequent decline in adult ringed seals becomes noticeable only in the second decade after the start of the steady decline in sea ice on which they depend; this time frame is actually at-hand given that in hind-sight west coast sea ice in Svalbard collapsed in 2006 (Vihtakari et al., 2018). The polar bear population would not be expected to enter into decline until the lack of recruitment of ringed seals results in the depletion of breeding aged ringed seals – starting in the third decade and dropping below the initial population size only after about 50 years. Indeed, the lack of suitable ice and snow conditions for ringed seal lairs might result in polar bears being able to prey on ringed seals in birthing areas more easily than in the past initially, because of increased densities of seals in the remaining land-fast sea ice areas (Rosing Asvid, 2006). Hunting success by polar bears will not decline until there are fewer seal pups in lairs and on open ice around the archipelagos.

Although lags between climate change and impacts on the fauna are expected, the sea ice conditions have already changed dramatically around Svalbard, and the collapse of this Arctic species assemblage might already be underway. Projecting the changes occurring to seals and bears in the broader Barents Sea Region is difficult because large-scale models of average ice cover in the Arctic do not provide the necessary specificity about the local ice (and snow) conditions that will matter most to the fauna. For ringed seal-polar bear dynamics, the critical ice environment is the extent of ice on the fjords in April and the snow cover over that ice (Kovacs et al., 2024). For other species, different but equally specific environmental conditions might be critical. The results of the sea ice in the Pacific Arctic retracting over the deep Arctic Ocean have been seen in vast changes to distribution of walruses, particularly mothers and calves. Mothers normally stayed on the off-shore ice through the summer, but with the retreat of the sea ice northward into the deep Arctic Ocean, females now use land-based haul-out sites along the coasts of Alaska and Russia (Jay et al., 2012). Stampedes in these new, mixed sex, high density haul-outs herds are resulting in increased calf mortality at levels that can negatively impact population demographics (Udevitz et al., 2012).

Although the general trends that we project are likely indicative of major changes to the ice dependent fauna of the Arctic, we acknowledge that the extent and rate of changes will be dependent on a number of factors that are as yet poorly known. Some of the key uncertainties about the system include: do individual ringed seals switch between breeding on land-fast sea ice and breeding on pack ice; are there two distinct breeding strategies such that the dynamics of the two subpopulations are largely independent; do polar bears have flexible enough prey selection to find alternative high-energy food adequate to raise cubs; how do changing ice conditions affect bearded seals; and are there interactions with other species in the system that can play key roles? Additionally, increased distance between land and the northern ice may have some implications for polar bears that have not been directly addressed in this study. Polar bears in the Barents Sea area depend on sea ice bridges providing access to denning areas on land during the fall, for females to give birth in mid-winter. Merkel and Aars (2022) showed that denning habitat is becoming less available (shown earlier by empirical capture data, Derocher et al., 2011) because sea ice no longer forms around islands in time to provide easy access to land. It is clear that there are already changes in bear distribution given that Maduna et al. (2021) described how genetic variability has decreased in Svalbard in recent years, as sea ice connecting the islands with the ice edge has been reduced, creating metapopulation structure that was not seen 30 years ago in this polar bear population.

We emphasize that the predictions arising from our metamodel are contingent on other aspects of Arctic community-function not being disrupted. We modeled only three of the ice-dependent Arctic species, we examined only the populations in the northern Barents Sea region, and we projected the impact of only one aspect of the sea ice environment (ice extent). Changing climatic conditions will undoubtedly have many more effects on these species than we have explored – due to interdependencies on other species, other features of the physical environment (freshening of fjords from glacial and riverine run-off), increasing acidification of Arctic water masses and other aspects of the species' biology. For example, the ringed seals mating system has been structured around males defending areas under the ice where several females have their (multiple) lairs. If the ice is not stable through the nursing period, it is likely that females will be much more mobile, with unknown effects on breeding behavior and pregnancy rates.

Changes to ice conditions are expected to cause cascading impacts throughout Arctic food webs, and we have not modeled possible effects of changing availability of prey for the seals. Freitas et al. (2008) suggested that foraging within drift ice areas north of Svalbard might not be energetically profitable for coastal ringed seals when sea ice retreats more than 700 km north of the islands in the archipelago. If this is true, and all ringed seals must feed in coastal areas, prey availability might become a limiting factor. Coastal ringed seals already show signs of retracting into very small refugia areas near tide-water glacier fronts (Hamilton et al., 2019), likely tracking their favorite food polar cod (*Boreogadus saida*) (Bengtsson et al., 2021). This small Arctic fish is already in decline in the Barents Sea area (ICES, 2018), likely because of Atlantification of the Barents Sea system (Fossheim et al., 2015). Other predators might also become more important, particularly the killer whale (*Orcinus orca*), which has already extended its range northward in the Northwest Atlantic Arctic (Higdon et al., 2014). New or increased competition from subarctic and temperate marine mammal species shifting their distributions northward are also a concern (Kovacs et al., 2011). However, some of these species may also contribute to alternative food sources for polar bears (which in our model we assumed to be constant). For example, walrus, harbor seal (*Phoca vitulina*), and reindeer populations have increased significantly in recent years in Svalbard (Kovacs et al., 2014; Le Moullec et al., 2019). Harbor seals are now hunted by polar bears in Svalbard and this species is definitely a climate winner that is expanding its range on the west coast of Svalbard (Merkel et al., 2013; Bengtsson et al., 2021). Recent data also indicate that bears are better at catching reindeer than was believed previously; they use several different techniques and kills have been documented in several areas of Svalbard (Stempniewicz et al., 2021). An important research need is to determine how flexible polar bears are with respect to switching to other prey species as the Arctic ecosystem changes in response to climate. Further, focus should be on the energetic value of alternative prey and if they can be sufficient to ensure survival and reproduction for Svalbard bears over time, with less availability of sea ice and the ice-associated seals.

Other areas of the Arctic might experience slower changes to the ice-dependent fauna than we predict for the Barents Sea. For example, some areas in Northwest Greenland might retain sea ice in the coming decades (ACIA, 2005). Such areas should be targeted for conservation of Arctic endemic species. The disruption and possible collapse of ecological communities dependent on specific climatic conditions can be expected in many places, even if these changes do not occur as quickly or as dramatically as is likely for ice-dependent species in the Barents Sea.

5 Conclusions

The risks of climate change to species and ecosystems are becoming increasingly well known, but they are still usually described as effects that will likely occur in the future. However, in parts of the Arctic, climate change has already exceeded the limits set by various climate protocols, and impacts on species are already occurring. The ice-dependent fauna of the Arctic is clearly especially vulnerable.

Climate change poses a special challenge to the Red List process used to identify species at risk (e.g., Akçakaya et al., 2014; Foden and Young, 2016). Our modeling suggests that noticeable species declines might not occur until several decades after the environmental changes that set in motion the ultimately threatening processes. Thus, observed population declines might be discovered too late to allow for conservation actions to attempt mitigation.

While the impacts of ongoing climate change on rare species with limited distributions are of concern, the ecological effects that result from collapse (even if not to extinction) of currently abundant species that are keystone species supporting ecological communities might be more pervasive and damaging to entire ecological communities. Multi-species models including predator-prey interactions, competition, and species dependencies are required to predict cascading effects of climate change on ecological communities. As more data become available on the species we modeled, other Arctic species, their interactions, the projections of climate change in the Arctic, and the effects of climate change on species and their inter-relationships, we expect that the metamodel approach we have used herein can serve as a template for further analyses that can generate more accurate and robust conclusions about the threats that climate change poses to species and ecological communities.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

RL: Formal analysis, Methodology, Software, Writing – original draft, Writing – review & editing. KK: Conceptualization, Data curation, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. CL: Data curation, Investigation, Writing – review & editing, Writing – original draft. JA: Data curation, Investigation, Writing – review & editing, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1439386/full#supplementary-material

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Linking habitat and population viability analysis models to account for vegetation dynamics, habitat fragmentation, and social behavior of a metapopulation of Florida scrub-jays

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Population dynamics and viability are driven by interactions among habitat and species biology. The Florida scrub-jay (*Aphelocoma coerulescens*) is a declining and Federally Threatened bird species that requires mid-succession habitat of partly open soil surface with mid-height vegetation. This habitat is created and sustained in a dynamic state of vegetation growth and periodic natural (e.g., fire) or managed (e.g., mechanical clearing) disturbances. Florida scrub-jays once occupied open oak scrub habitats across much of peninsular Florida but have been reduced to a few regional metapopulations and scattered isolated remnant populations. Many of these populations are undergoing continuing decline as open scrub is either converted to residential development or transitions into closed pine and oak forests due to fire suppression. Long-term field studies have shown that breeding and survival rates are determined by the quality of the scrub habitat, with the demography influenced by and in turn mediating the social structure. Prior Population Viability Analyses (PVA) that included dependencies of demographic rates on habitat and social structure indicated that the east coast Florida metapopulations were fragmented into remnant protected patches that were too small and isolated to support long-term persistence, even if the remaining habitat area and quality was sustained. Moreover, recent modeling of habitat transitions under various proposed management schemes, in conjunction with implementation of Adaptive Resource Management (ARM), projected that the proportion of optimal habitat will continue to decline. In this study, we integrated these habitat projections within the PVA and found that the Brevard County mainland metapopulation is projected to decline toward extinction unless habitat quality, extent, and connectivity can be improved. Land managers have recently implemented new innovative methods for restoring optimal scrub habitat, identifying potential improvements in habitat connectivity of nearby populations, and translocation methods to increase and reinforce the demographic and genetic integrity of local populations. Our linked habitat-population models project that the combination of such habitat and population management actions can stabilize the metapopulation and achieve long-term viability.

KEYWORDS

habitat modeling, habitat management, population viability analysis, Florida scrub-jay, population management, adaptive resource management, species recovery

1 Introduction

The transitional habitat dynamics of species of conservation concern often need planning and active management. Active management is especially important for species in fragmented landscapes that once depended on lightning fires that can no longer spread naturally across landscapes. However, these managed replacements often differ greatly from natural fires in seasonality, intensity, and frequency and often need supplemental mechanical treatments to achieve the same outcome as natural disturbances (Duncan et al., 2009, Duncan et al., 2015).

There is uncertainty in adaptive management of such systems where actions and models of predicted effects need to be repeatedly revisited and adjusted (Nichols et al., 2024). Adaptive Resource Management (ARM) models support management by estimating the most appropriate management actions based on habitat (e.g., successional states) and occupancy (e.g., territory occupancy) states (Eaton et al., 2021), abundance, or vital rates (Johnson et al., 2011). In addition, endangered species recovery planning entails population analyses to estimate time for species recovery and potential population strategies required for long-term sustainability (Population Viability Analyses, PVA).

However, both habitat and population dynamics are often characterized too simply for guiding effective management. Habitat is sometimes described only as types of landcover where a species is found, but habitat is not likely to depend on a single property of the environment, nor will it often be spatially uniform. Habitat should refer to conditions relevant to both occupancy of species and the demographics (recruitment, survival) that support sustainable populations (Van Horne, 1983; Hall et al., 1997). Most PVA make projections based on demographic rates recorded over a series of years with implicit or explicit assumptions that the birth rates, death rates, and habitat quality will remain the same as in years when data were collected. To account for ongoing or projected changes to the environment, a PVA should include both the projected changes to the habitat and links of habitat to demography (fecundity, survival, dispersal, and carrying capacity). The extent to which the PVA considers the key features and dynamics of habitat will determine the usefulness of the PVA for projecting trends, assessing threats, and evaluating management options.

The Florida scrub-jay (*Aphelocoma coerulescens*, FSJ) is a declining and Federally Threatened bird species endemic to Florida, USA. Much about FSJ sociobiology, population parameters, and habitat requirements has been the result of long-term studies of two distinct metapopulations, one study now exceeding 45 years (Woolfenden and Fitzpatrick, 1984; Fitzpatrick and Bowman, 2016) and the other over 35 years (Breininger et al., 2009, Breininger et al., 2023). These studies show that FSJs generally mate for life and stay within the same territory once they become breeders (Woolfenden and Fitzpatrick, 1984; Fitzpatrick and Bowman, 2016). Florida scrub-jays are cooperative breeders where young usually remain with their parents for several years helping feed new offspring, defend territories, and spot and mob predators. Nonbreeders quickly fill nearby breeder vacancies and rarely disperse more than a few kilometers from their natal territory (Breininger et al., 2006, Breininger et al., 2023). Florida scrub-jays require oak scrub (*Quercus* spp.) that occurs on dry sandy ridges often within a landscape of mesic flatwoods (saw palmetto) and ephemerally flooded marshes within areas subject to fires caused by lightning. Transitions between habitat states vary depending on vegetation assemblages, climatic conditions, habitat edge effects, fire history, and mechanical cutting in manners that influence territory occupancy, abundance, reproductive success, and survival (Breininger et al., 2010, Breininger et al., 2018; Johnson et al., 2011; Eaton et al., 2021). The 45-year study (at Archbold Biological Station) focused on relatively stable, optimal habitat, whereas the 35-year study (on Kennedy Space Center, Merritt Island National Wildlife Refuge, and nearby mainland Brevard County) occurred in conservation areas degraded by reductions in the fire regime and where restoration has been a difficult process. Degradation resulted in spatially and temporally dynamic patterns in habitat quality where territory quality varied greatly within landscapes.

A revised U.S. Fish and Wildlife Service species recovery plan was approved in 2019 (U.S. Fish and Wildlife Service, 2019a) based on a triage strategy identifying areas known as “focal landscapes” that have the potential for long-term population viability. Three criteria for delisting the species are: (1) stable or increasing populations in each of 7 focal landscapes (one of which, the East Coastal Genetic Unit, coincides with the South & Central Mainland Brevard County metapopulation that is the focus of this study); (2) subpopulations "connected to the extent that natural genetic diversity can be naturally maintained without translocations"; and (3) threats "addressed such that sufficient habitat remains for the species to remain viable for the foreseeable future." The first criterion requires that the decline over the last few decades be halted or even reversed. The second criterion implies minimal loss of genetic diversity, but it does not define what low level of loss might be accepted. Retaining at least 95% of genetic diversity would be approximately equivalent to avoiding inbreeding at the level of first-cousin matings (F = 0.0625) or closer. The third criterion directly addresses the need for habitat protection and management, but it does not define what is considered to be "viable" (other than the first two criteria), nor does it define the duration of the "foreseeable future". A large majority of the U.S. Fish & Wildlife Service recovery plans that provide explicit definitions of viability have used a criterion of keeping the probability of extinction below 5% for 100 years (Carroll et al., 2019).

This paper focuses on the South and Central Mainland FSJ metapopulation (as denoted by Stith, 1999; and shown in Figure 1) in Brevard County, Florida, USA. This metapopulation occupies habitats that are mostly protected and managed by the county Environmentally Endangered Lands program. Prior Population Viability Analyses (Lacy and Breininger, 2021) assessed the viability of this and also the North Mainland and Canaveral

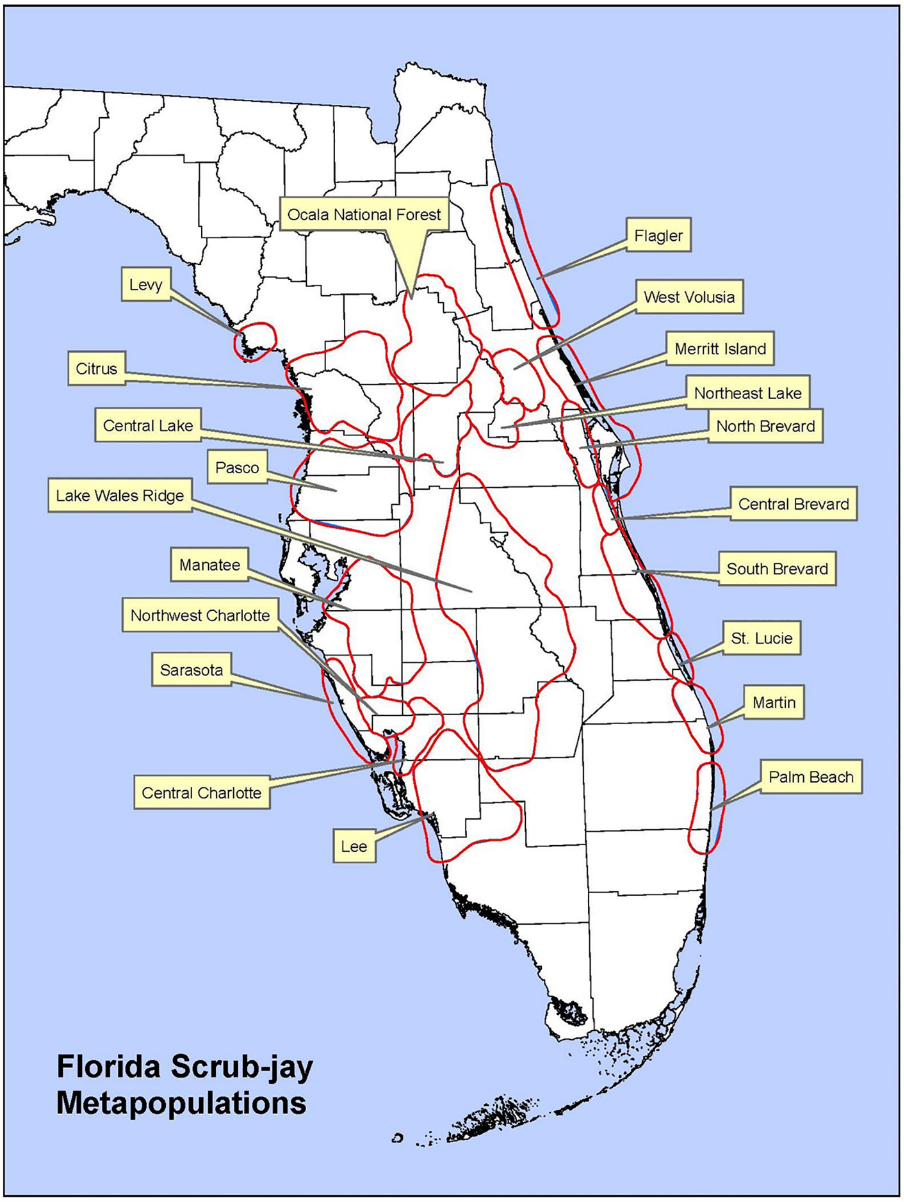

FIGURE 1
Florida scrub-jay metapopulations. From U.S. Fish and Wildlife Service (2019b).

metapopulations in Brevard County, but without consideration of the changing habitat conditions caused by vegetation succession, natural disturbances, and management actions. Several earlier PVA models assumed static habitat that was identical across populations, excluded genetics, and were not individual-based (e.g., Woolfenden and Fitzpatrick, 1991; Root, 1998; Breininger et al., 1999). Stith (1999) developed an individual-based model distinguishing suburban and conservation lands that were assumed to be optimal habitat from unsuitable urban areas. Florida scrub-jay territories within conservation lands often occur as mixtures of habitat that do not transition between states uniformly and where territories function as sources and sinks within individual populations (Breininger and Carter, 2003; Breininger and Oddy, 2004; Breininger et al., 2009, Breininger et al., 2023). These complexities inspired collaborations among stakeholders, land managers, and biologists to develop ARM projects to enhance species recovery (Johnson et al., 2011; Eaton et al., 2021).

Management of threatened species usually focuses either on habitat projections and options or on population viability assessments and actions to improve population demography. Even when both habitat and population dynamics are considered, the analyses are usually independent, and the resulting actions considered as alternatives rather than as an integrated strategy. The earlier PVA on this FSJ metapopulation concluded that it was comprised of populations that were all too small and isolated to support long-term persistence (Lacy and Breininger, 2021), while the habitat modeling presented a bleak picture of projected decline in the quality of the remaining patches of habitat (Eaton et al., 2021). Neither approach identified a strategy that was likely to restore adequate habitat and recover this metapopulation. This study integrates updated habitat projections from the ARM project within the PVA to account for ongoing or projected changes to the environment and links habitat to demography. This linked habitat-population model provides new insights into how the combination of habitat and population management actions can stabilize the metapopulation and achieve long-term viability.

2 Methods

Many of the methods here are based on population sizes (tallied as number of breeding groups), estimates of demographic rates, and dispersal rates parameterized and assembled in a recent PVA (Lacy and Breininger, 2021) based on >30 years research and monitoring that has occurred in the east coast Florida metapopulations of the FSJ. These previous studies are well characterized in dozens of published articles (e.g., Breininger et al., 2009, Breininger et al., 2023; Breininger and Oddy, 2004; and see Introduction). Key features are summarized below.

2.1 Population delineation and habitat classification

Fourteen populations were delimited by identifying those habitat areas that were separated by at least 667 m at the closest points or are closer but separated by barriers to dispersal. Florida scrub-jays occasionally disperse across greater distances, but observed inter-population dispersal is insufficient to lead to genetic panmixia or regular demographic reinforcement (Lacy and Breininger, 2021). The metapopulation in south and central Brevard County mainland has not been observed to exchange individuals with either of two adjacent metapopulations – a much smaller north Brevard metapopulation or a Canaveral/Merritt Island metapopulation.

Established breeding pairs rarely move their territory, other than adjusting boundaries in response to opportunities and inter-group conflicts, and breeding pairs have not been observed to disperse between populations (Breininger et al., 2006). Dispersal rates of helper jays between each pair of populations were determined from the number of observed movements of banded helper jays from the natal population to a destination population, where they usually attempted to become breeders. Frequencies of movements relative to the total bird-years of banded helpers were used to create a matrix of inter-population dispersal rates (Lacy and Breininger, 2021).

As a component of the ARM program, FSJ habitat across the subpopulations in southern and central mainland Brevard County has been assessed by land managers and local biologists annually since 1997 (Eaton et al., 2021). The extent of accessible habitat in each population was overlaid with a total of 249 grid cells of 10 ha, approximating the size of scrub-jay territories. These grid cells will be referred to and treated in our model as “potential territories” (Breininger et al., 2006). The number of grid cells of suitable habitat was used to estimate the carrying capacity (K) for breeding groups in each population, except that three populations received supplemental feeding from park visitors resulting in smaller breeding territories, increasing local population sizes. For these food-supplemented populations, carrying capacity was estimated to be the current number of breeding groups because they showed elevated fecundity and no evidence of density-dependent reductions in survival (Breininger et al., 2022, Breininger et al., 2023). The resulting total metapopulation size (K) was 266 potential territories, with 168 of these occupied by breeding groups in 2023.

Analysis of wildlife habitat requires dual consideration of the characteristics of the environment that are changing and potentially modified through management and the consequent quality of that environment as habitat for the species (Nichols et al., 2024). Potential territories have been classified into five habitat states defined by vegetation height and extent of ground cover (Breininger et al., 2014; Eaton et al., 2021). Habitat states were consolidated and renamed to describe quality with respect to FSJ demography (Breininger et al., 2010; U.S. Fish and Wildlife Service, 2019b) and these simplified categories were used in the PVA (Lacy and Breininger, 2021). “Optimal Open” (OpO) habitat had medium-height (1.2 to 1.7 m) oak scrub and open sandy areas interspersed between scrub patches. This habitat state was named “Strong” with respect to its suitability for FSJs when it was determined that this habitat supported the best reproduction and survival (Breininger et al., 2009, Breininger et al., 2014, Breininger et al., 2023), with an estimated 7.0% potential population growth per year (Table 1). “Optimal Closed” (OpC) habitat had similar

TABLE 1 Mean demographic rates and annual fluctuations (EV) in those rates for Strong, Weak, and Sink FSJ habitat.

	Strong	Weak	Sink	EV
BrSucc-H	0.498	0.355	0.302	0.154
BrSucc-NoH	0.465	0.286	0.237	0.154
Brood-H	2.282	2.065	1.934	
Brood-NoH	2.278	1.936	1.843	
JuvMort	0.344	0.316	0.421	0.183
HelperMort	0.257	0.273	0.316	0.064
BrMort	0.171	0.204	0.229	0.062
Pop. Growth (r)	0.070	-0.029	-0.104	

BrSucc-H: Breeding success (probability of producing a brood) for pairs with at least one helper
BrSucc-NoH: Breeding success (probability of producing a brood) for pairs with no helpers
Brood-H: Mean brood size (number juveniles produced) for pairs with at least one helper
Brood-NoH: Mean brood size (number juveniles produced) for pairs with no helpers
JuvMort: First year mortality
HelperMort: Annual mortality of helpers
BrMort: Annual mortality of breeders
Pop. Growth (r): exponential population growth averaged across years 1-5 of a simulation of a hypothetical large population (without inbreeding depression or EV) in that habitat state.

height oak scrub but with few open sandy areas. It was named "Weak" owing to the lower reproduction and survival in this habitat, resulting in projected population decline of 2.9% per year. "Short" (Sh) sites had vegetation that was mostly below 1.2 m. "Tall-mixed" (TM) had short or medium-height scrub with patches of oak > 1.7 m in height and > 0.4 ha in size. "Tall" (T) had patches of oak > 1.7 m in height and > 0.4 ha in area, and no short or medium-height scrub or open areas. Sh, TM, and T vegetation were named collectively as "Sink" habitat, as they have lower reproduction and survival (Breininger et al., 2014), resulting in a projected 10.4% decline per year. We will use the five vegetation labels (Sh, OpO, OpC, TM, and T) when describing projections of vegetation dynamics, and the three habitat quality labels (Strong, Weak, and Sink) when describing consequences for FSJ demography.

Population projections were made for both hypothetical isolated populations (for testing effects of model parameters) and for the actual configuration of 14 populations in the metapopulation, with occasional inter-population dispersal as estimated from a distance function derived from data on inter-population movement frequencies (see below). For the analyses of isolated populations varying from 50 to 300 potential territories, the initial distribution of habitat states was set to the observed distribution across the metapopulation (0.492 OpO, 0.053 OpC, 0.094 Sh, 0.353 TM, 0.008 T) tallied in 2023 surveys by local biologists and land managers, resulting in 0.492 Strong, 0.053 Weak, and 0.455 Sink habitat with respect to the quality affecting the FSJ demography. The initial proportion of potential territories in each state occupied by breeding groups was similarly set to the metapopulation means observed in 2023 (0.847 of Strong, 0.786 of Weak, 0.380 of Sink; and 0.632 of all potential territories occupied). In analyses of the actual metapopulation, for each local population the initial number of potential territories in each of the five habitat states and the numbers occupied by breeding groups was set to the observed 2023 counts, using methods described by Eaton et al. (2021).

Due to successful implementation of new habitat management methods, the number of OpO potential territories increased dramatically from 2018 (n = 80) to 2023 (n = 131), accompanied by a parallel increase in breeding groups (111 to 168; 8.6% growth per year) in the metapopulation. To provide comparisons to the projections of habitat distributions and occupancy made by Eaton et al. (2021) based on data as of 2018, we also examined scenarios that started the distribution of habitat states (0.330 OpO, 0.116 OpC, 0.067 Sh, 0.446 TM, 0.041 T) and the occupancies of the states for each local population to the values that were observed in 2018.

2.2 Population demography

Components of reproductive success (% pairs producing juveniles, number of juveniles produced per pair) and survival rates were tallied from the long-term studies beginning in 1998 that include a census every month (Breininger et al., 2006, Breininger et al., 2009, Breininger et al., 2014, Breininger et al., 2023; Carter et al., 2023). Demographic rates were tallied each year from 1988 through 2021, separately for Strong, Weak, and Sink habitats, and separately for breeding pairs with no helpers vs with helpers (Table 1). Monthly detection probabilities for the field surveys that contributed to the estimation of demographic rates are usually greater than 0.90 using mark-recapture methodologies (Breininger et al., 2009, Breininger and Carter, 2003; Carter et al., 2023), so we used direct calculations of monitored groups rather than estimating rates from mark-recapture studies for a subset of years, as described by Lacy and Breininger (2021). For each level of habitat quality (Strong, Weak, and Sink), we estimated the annual variation in demographic rates due to fluctuations in the environmental conditions (the "environmental variation", EV), by removing the expected binomial sampling variation from the total inter-annual variation in the data (Akçakaya, 2002; Lacy et al., 2023). Differences among Strong, Weak, and Sink habitats in EV for each demographic rate were non-significant, so each EV was pooled across habitats.

It was assumed that each local population was panmictic, other than for the avoidance of close inbreeding (see below), as the distances across each population can easily and readily be traversed by FSJs. However, FSJs most often establish new territories adjacent to (or sometimes budded off from) their natal breeding group (Breininger et al., 2006, Breininger et al., 2023), so it is possible that some localized inbreeding occurs above that generated in the simulation based on local population sizes and within-population breeding opportunities.

Inter-population dispersal rates were estimated from observed movements of FSJs from 1997 to 2008 (Breininger et al., 2006). Dispersal is almost exclusively departures of helper jays from their natal territories, after which they attempt to become established as breeders. Regression models were used to determine what function best fit the relationship of distance between nearest points for each pair of populations (D, in km) to dispersal rate (R) as the probability of a helper moving to the other population. The observed frequency of inter-population dispersal was found to be best fit with an inverse square-root model, with a regression equation of $R = 0.0275/(\sqrt{D})$, ($SE(slope) = 0.0051$; $P < 0.00001$, $R^2 = 0.1845$) (Lacy and Breininger, 2021).

Florida scrub-jays are assumed to avoid mating with parents, offspring, siblings, maternal half-siblings, or paternal half-siblings (i.e., members of their breeding group), and we included this restriction on matings in the PVA model. We modeled any impacts of lower levels of inbreeding or accumulated inbreeding as a decrease in juvenile survival for inbred offspring, with the severity of inbreeding depression as estimated by Chen et al. (2016) (7.478 Lethal Equivalents for impacts on survival from 11-day nestling to yearling).

The prior PVA emphasized that local populations are currently too small and too isolated to ensure metapopulation viability, due to both demographic and genetic instability (Lacy and Breininger, 2021). Inter-population dispersal can be increased via habitat improvements, including both expansion of suitable habitat accessible to some populations and creation of corridors between some local populations, and via new experimental managed translocation of FSJs. To explore the value of increased connectivity, we examined some scenarios that included 3-fold or 5-fold more dispersal between each pair of populations.

The effect of habitat on overall population growth and persistence depends on both the extent of available habitat (number of potential breeding territories) and the distribution of habitat quality (Strong, Weak, and Sink). Florida scrub-jays respond to the availability of optimal habitat both in the likelihood of helpers leaving a natal group and attempting to become breeders in their own territory and in the likelihood that such new breeders will establish their new territory in optimal vs suboptimal habitat. The probability of a female helper transitioning to be a breeder was modeled as a logistic function: Pr[HtoBr] = exp(-1+B*pAvail)/[1 + exp(-1+B*pAvail)], with pAvail being the proportion of Strong potential territories unoccupied, and the slope parameter B defining the strength of the relationship. Male helpers were assumed to leave their natal groups to respond to opportunities to pair with females that were either transitioning from helpers to occupy new territories or were established breeders whose mates had died.

Next, the likelihood that a new breeder will establish her territory in Strong habitat was modeled by assuming that the female would choose a territory with Strong habitat with probability = pStrong^(1/Pref), with pStrong being the proportion of unoccupied territories that were Strong, and Pref being a parameter fitted to generate the observed proportion of occupied territories in Strong habitat. If a new breeder does not select a Strong territory in the simulation, then she is assigned to a Weak territory (rather than Sink) with probability equal to a similar exponential function of the proportion of Weak available territories among those that are not Strong: [pWeak/(1 – pStrong)]^(1/Pref). If neither Strong nor Weak are selected, then a new breeder is assigned to a Sink territory. Note that the likelihood of a new breeder establishing a territory in available Strong habitat might be not due only to the strength of behavioral preference for Strong habitat. The selection of a new territory might also be determined by the ability of the FSJs (and the researchers) to identify what is and will remain as the best habitat, and the accessibility of unoccupied Strong habitat. (E.g., even if Strong would be preferred, females transitioning to breeders might search for vacant habitat only close to their natal territory, and thereby end up settling in Weak habitat.)

After becoming breeders in new territories, jays were assumed not to revert to helper status and to remain in territories with the same habitat quality until they died.

Carrying capacity was imposed via a ceiling that removed helpers randomly if the population size exceeded 4 times the number of potential territories. The mean number of helpers per breeding group almost never exceeded 2 in our simulations, so this ceiling had no effect on population projections. However, a functional carrying capacity arises in our model mechanistically, in that as Strong territories become more fully occupied, fewer helpers transition to breeding status, and any new breeders are forced into suboptimal habitat with reproduction and survival rates that result in population decline in those Weak and Sink habitats.

2.3 Sensitivity analyses

Several of the variables that describe the behaviors of the scrub-jays in our models could not be estimated directly from available field observations, including the parameters that describe the probability that a helper will disperse from its natal group and attempt to become a breeder (parameter B) and the probability that such new breeders will establish territories in Strong vs Weak vs Sink habitat (Pref) – with both used in functions of the availability of vacant territories in each habitat state (see above). The baseline values of these parameters (B = 6, Pref = 6) were obtained by testing a range to see what values would result in populations with the helper:breeder ratio and proportional occupancies of Strong, Weak, and Sink habitat that approximate ratios observed in the field (Lacy and Breininger, 2021). For both parameters, we tested a range of 2 to 10 to determine how these aspects of FSJ social behaviors influence population viability and how sensitive the population projections are to the specific values chosen.

The sensitivity of results to estimated values of other model parameters (lethal equivalents, breeding success, juvenile and adult mortalities, and EV in reproductive and mortality rates) were examined in the prior PVA (Lacy and Breininger, 2021). While some (especially adult mortality) impacted population growth or probability of local extinction, within ranges considered plausible they were not found to have large effects on the relative comparisons among scenarios testing population structure and management options, and precise values assumed for each variable did not affect general conclusions about metapopulation viability and management recommendations.

2.4 Habitat projections

We projected changes in the number of Sh, OpO, OpC, TM, and T potential territories in each population over up to 100 years, starting with the distribution of habitat types observed in 2023, by applying the transition probabilities derived by Eaton et al. (2021) for each of four habitat management regimes (BURN, LMB, HMB, and NONE) applied in Oak woodland sites. The BURN regime used prescribed burning to maintain scrub vegetation. Light mechanical cutting followed by burning (LMB regime) employed cutting of taller vegetation to increase its flammability followed by a prescribed burn. Heavy mechanical cutting followed by burning (HMB regime) employs more extensive cutting of taller vegetation that would otherwise escape burning, followed by a controlled burn. The NONE regime applied no management to a site, allowing natural succession to occur. We applied BURN, LMB, and HMB regimes every 5 years, with intervening years subjected to no management. Each population, in each iteration, was assigned a random year from 1 to 5 as the first year for management to be applied. We also examined some scenarios with application of management actions on 3-year rotations. See Eaton et al. (2021) for more details on the management regimes that were explored and Nichols et al. (2024) for detailed discussion of the estimation of state transitions and the use of the projections in adaptive habitat management. We modeled transitions between habitat states probabilistically, with the fate of each potential territory sampled from the multinomial distribution determined for transition from its present state to its state in the subsequent year.

Managers have been exploring new techniques to improve habitat quality, and one new method (which we label DINO) uses an excavator with a forestry mulching attachment, commonly referred to as a brontosaurus mulcher (https://brownforestryproducts.com/), that reduces tall scrub to optimal height. This method has been most successful at transitioning TM to OpO in an annual time step resulting in a doubling of FSJ local population sizes in 2-3 years in several sites (Breininger, unpublished data). To represent the plausible effects of this new management regime, we tested scenarios that have much greater probabilities of transition from TM to OpO, given that this approach has been found to be much more successful for creating optimal habitat than was projected for any of the four previous management regimes (Eaton et al., 2021). The DINO method is meant to supplement the use of fire because mechanical cutting of tall scrub is often first needed prior to burning (Schmalzer and Boyle, 1998). For the DINO regime, we use a set of habitat transition probabilities that plausibly represents the new system being used by land managers (Supplementary Table S1).

2.5 Vortex PVA model

The FSJ population dynamics were modeled using the Vortex (version 10.7.0) population viability analysis software (Lacy, 2000a; Lacy et al., 2023; Lacy and Pollak, 2024; software and manual available at https://scti.tools/vortex/). Vortex is an individual-based model that simulates the fate of each individual through an annual cycle of breeding, mortality, increment of age, dispersal among subpopulations, removals (or emigration from the population), supplements (managed or natural immigration), translocations, and truncation if the population exceeds the carrying capacity (ceiling density dependence). Stochasticity in demographic processes is modeled as annual variation in each demographic rate at the population level (environmental variation) and random sampling variation in the fates of individuals (demographic stochasticity) (Lacy, 2000a, Lacy, 2000b). Individual fates are summed to provide projected population sizes, population growth rates, population age and sex structure, and probabilities and times to local extinction. Vortex projects the effects of population size and structure on loss of genetic diversity, and in turn the impacts of loss of diversity on fecundity and survival (inbreeding depression). Vortex provides the flexibility to specify demographic parameters as functions of environmental (e.g., climate, prey base), population (e.g., density, social structure), or individual (e.g., age, social status, inbreeding, genotype) properties through the use of state variables to track properties of the system (Global State Variables), each local population (Population State Variables), and each individual animal (Individual State Variables).

Details of the Vortex model structure and parameter values used to model the complex demographic, social, and other population processes driving FSJ population trajectories are given in a report of the earlier PVA that did not include linking to dynamic projections of habitat, but instead tested scenarios with various fixed values for the distribution of habitat quality in each population (Lacy and Breininger, 2021). Projections were run for 100 years, with 500 independent iterations of the population trajectories in each scenario. Tests with more iterations showed that 500 iterations provided adequate precision of means and variances to allow for comparison among scenarios.

2.6 Measures of metapopulation viability

We assessed metapopulation viability by the population size (number of breeding groups), probability of metapopulation persistence, median time to extinction (when extinction probabilities exceed 50%), quasi-extinction (probability that the population declined below 10 breeding groups), and the proportion of initial gene diversity remaining and the inbreeding coefficient averaged across those iterations in which the metapopulation was not extinct. We present population trends as the number of breeding groups, quasi-extinction, and mean genetic metrics over the first 50 years. The 50-year time frame is likely longer than the planning and management focus, but such projections can be useful because longer term consequences might not be apparent for decades, even if processes that will lead to demographic and genetic decline are underway earlier. The final extinction of a population in decline can take even longer, so the probabilities that the population will be extinct (reduced to no animals or just one sex) are presented over the full 100-year projections.

2.7 Integrating habitat transitions into the PVA

The inclusion of habitat projections as drivers of demography in the Vortex population model was implemented by specifying the habitat transitions each year within macros. The macros step through each potential territory, each simulation year, and determine its next habitat state by sampling the multinomial transition probabilities. In addition to the scenarios simulating five management regimes (BURN, LMB, HMB, NONE, and DINO), a "NoHab" scenario was modeled in which habitat remained constant at the distribution of states observed in 2023 (with neither management nor natural transitions of vegetation). The Vortex project files, data files accessed in the Vortex scenarios, and macros used in the Vortex model to implement habitat projections are available in a Zenodo repository at 10.5281/zenodo.13850866.

2.8 Population management options

Four population management options and combinations of them were explored to determine if they would slow, prevent, or reverse decline of the breeding population and ensure long-term viability of the metapopulation. These options for managing the FSJs and the configuration of populations were applied on top of an assumption that the improved management of habitat, represented by the DINO scenario, would be used into the future.

A "Connect" scenario assumes that several sets of populations can be functionally merged through protection and restoration of corridors of habitat. The connected populations are Jordan + Valkaria + Malabar (creating a single population of currently 42 breeding groups in an area that can support 78 territories), N Sebastian Conservation Area + Coraci + N Fork (creating a population of 43 breeding groups in an area that can support 50 territories), and Carson Platt + Corrigan (creating a population of currently 24 breeding groups in an area that can support 46 territories). These merged populations would be larger than any of the existing populations which have a maximum size of 34 potential territories (see Supplementary Table S2).

Two scenarios, "Dx3" and "Dx5", assume that inter-population dispersal can be increased 3-fold or 5-fold relative to the distance-dependent estimates from prior observed dispersal rates. Such increased dispersal might be achieved through increased protection of intervening landscapes or might occur as a result of populations becoming more saturated causing more birds to disperse from natal populations.

Two translocation scenarios tested the impact of translocation of FSJs among populations. A total of 15 or 30 FSJs were translocated each year in scenarios "Trans15" and "Trans30", with the number of jays removed from each donor population proportional to the number of occupied Strong territories in that population, and the number of FSJs moved into each recipient population proportional to the number of unoccupied Strong territories in the recipient population. For example, if one population has 20 occupied Strong territories out of 100 total in the metapopulation, then 6 of the 30 FSJs selected to be translocated in the Trans30 scenario would be taken from that population. If a second population had 10 of 60 unoccupied Strong territories, then it would receive 5 of the 30 translocated FSJs. Fractional numbers were stochastically rounded, and the scrub-jays to be moved from each population were chosen at random on the assumption that capture of FSJs for translocation would not be able to target specific birds.

A "Feed" scenario assumes that 1.5x more breeding groups can occupy a given area of Strong habitat if they are provided with supplemental feeding. Increases in numbers above what can be supported in 10 ha of habitat (the estimated mean territory size in the absence of feeding) have been observed in three populations (Viera, N Sebastian Conservation Area, and Wabasso) that do receive supplemental food from visitors, partly because of increased fecundity and density without evidence of decreased survival (Breininger et al., 2022; Breininger et al., 2023).

All combinations of Connect, Trans15 or Trans30, and Feed options were also assessed (Supplementary Table S4).

3 Results

3.1 Baseline projections in the absence of habitat transitions

Simulations of hypothetical isolated populations in habitat that can support 100 territories (i.e., 1000 ha of contiguous habitat), initially 50% occupied by breeding groups, confirmed that the demographic rates observed in territories with Optimal Open habitat (OpO, deemed "Strong") result in positive population growth (mean exponential growth over first 5 years of simulations: $r = 0.060$). Optimal Closed habitat (OpC, deemed "Weak") does not support positive growth ($r = -0.043$). Short, Tall Mix, and Tall (collectively deemed "Sink") results in faster population declines ($r = -0.120$) and extinction usually occurred within 15 to 30 years (Figure 2). These growth rates are all lower than projected in Table 1, because of stochastic effects in the smaller populations. Larger populations in Weak and Sink habitat persisted a few years longer, but ultimately suffered the same fate, with median times to extinction of 52 and 29 years for populations with 300 potential territories (3000 ha) of Weak or Sink habitat, respectively (Supplementary Figure S1). Although the separation among populations in Strong, Weak, and Sink habitat is clear for the mean population trajectories, there was considerable stochastic variation among the independent iterations (as shown by the +/- 1 SD dashed lines in Figure 2A).

Simulations of populations in all Strong habitat able to support from 25 to 250 potential territories, initially 50% occupied, showed rapid initial population growth, followed by stability with most or all habitat occupied when there were 75 or more potential territories (Supplementary Figure S2A), and few or no extinctions occurred within 100 years if the total area of habitat was more than 75 potential territories (Supplementary Figure S2B).

Simulations of isolated populations of varying size, each with the current (2023) proportions of Strong (49.2%), Weak (5.3%), and Sink (45.5%) habitat and proportions initially occupied (84.7%, 78.6%, and 38.0%, respectively), showed that the populations with this mix of habitat states are projected to decline slowly, as the number of breeding groups in Sink and Weak habitats declines (Supplementary Figure S3A). A population with fewer than about 150 to 175 potential

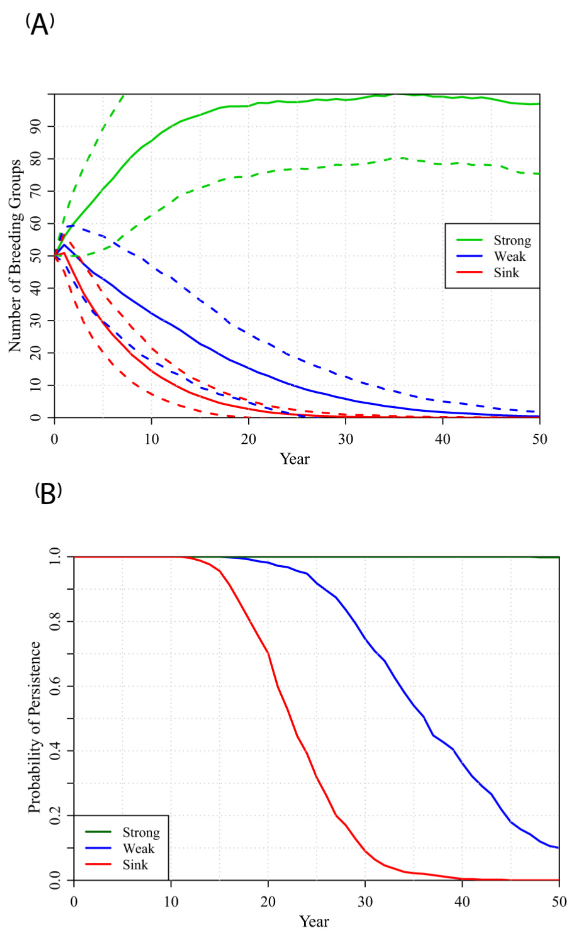

FIGURE 2
Mean trajectories projected over 50 years for populations in 100 potential territories, with initially 50 occupied, of all Strong, Weak, or Sink habitat (top to bottom, respectively): **(A)** number of breeding groups, with +/- 1 SD range across iterations shown as dashed lines; **(B)** probability that the population persists.

territories (74 to 86 in Strong habitat) is vulnerable to extinction within 100 years (Supplementary Figure S3B). Very small, isolated populations, with only 25 potential territories, have a median time to extinction of 46 years. Ten of the 14 existing local populations have fewer than 25 potential territories, and all 14 have fewer than 35, so larger areas of contiguous habitat or increased connectivity among the populations will be necessary for long-term conservation.

Simulation of the current (2023) configuration of 14 populations with a total of 266 potential territories, under an assumption that habitat will remain as it is (the NoHab scenario), projected steady decline of the metapopulation, with a few local populations remaining stable or growing (primarily as a result of immigration from nearby larger populations), and most populations declining (Figure 3A). All populations had some chance of extirpation within 50 years (Figure 3B). The probability of metapopulation extinction within 50 years was less than 1%, but was 67% over 100 years, as the mostly isolated populations become increasingly inbred.

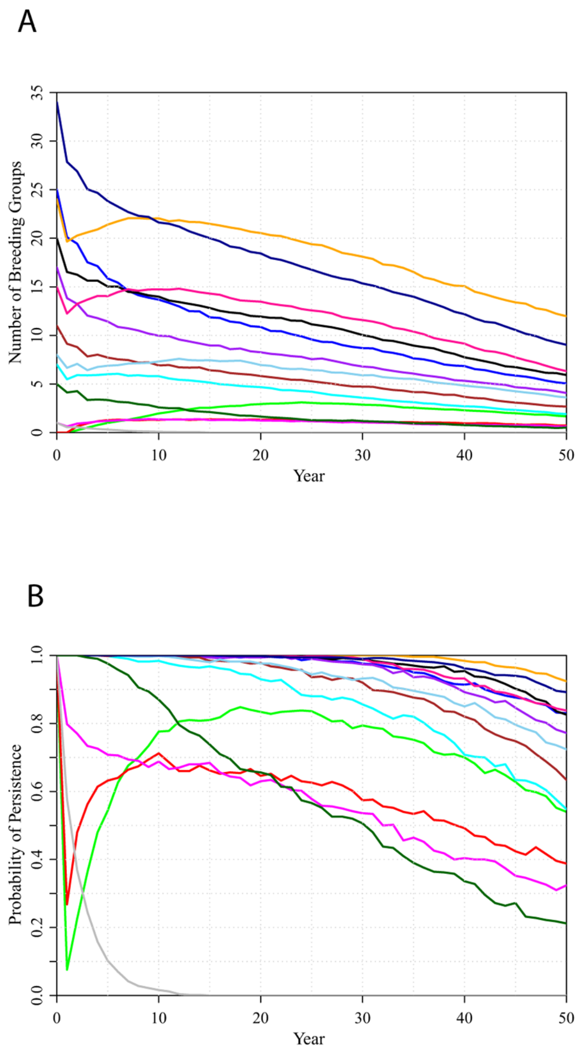

FIGURE 3
Trajectories projected over 50 years for the 14 populations comprising the metapopulation, under the assumption that proportions of Strong, Weak, and Sink potential territories remain constant (NoHab scenario): **(A)** number of breeding groups; **(B)** probability the population persists.

3.2 Habitat projections

Supplementary Figure S4 shows projected proportions of each habitat state under the five management regimes and the scenario of no habitat change. BURN management leads to more optimal (OpO) habitat and less sink habitat (predominantly TM) than do LMB or HMB, and each of these management regimes outperforms a lack of active management (NONE scenario). All four of these scenarios project long-term proportions of the habitat states that are similar to the steady state proportions projected by Eaton et al. (2021). However, these management regimes all predict that much of the currently OpO habitat will convert to TM (and to a lesser extent to OpC), with projections that the current nearly 50% OpO will decline to about 20% over the next 15 years (three cycles of active management). A lack of management (NONE) results in only about 11% remaining in optimal (OpO) state. In contrast, as a result of new management methods being applied since 2018, the metapopulation trend over the past 5 years has been the reverse, increasing from 33% to 49% OpO, while Weak (OpC) decreased from 12% to 5%, and Sink (Sh + TM + T) decreased from 55% to 45%. We do not yet have data sufficient to estimate transition probabilities for the newly implemented management, but sets of transition probabilities that increase OpO (e.g., the DINO scenario; Supplementary Table S1) can approximately mimic the changes that occurred in the past five years, and they result in a steady state distribution that maintains proportions of Strong, Weak, and Sink habitats close to those observed in 2023 (Supplementary Figure S4). For example, the decrease in TM projected from 2018 with the DINO transition probabilities almost exactly matched the projection starting with 2023 proportions beginning 5 years later (Supplementary Figure S5). The projections starting with the 2018 distributions of habitat drop in 5 years to the proportion observed in 2023, indicating that the DINO transition probabilities mimic the reduction in TM that was achieved by improved management methods.

3.3 Population projections in a dynamic habitat

The metapopulation is expected to decline to 23% occupancy (equivalent to about half of Strong habitat occupied) within 50 years if habitat is assumed to remain as it is in 2023 (Figure 4: top line, NoHab scenario), updating the analyses done previously (Lacy and Breininger, 2021). The metapopulation is expected to persist for 50 years, but then be at increasing probability of extinction over the following 50 years (Figure 4B). Under no active management (NONE scenario: bottom, blue lines), population decline is more rapid and there is a 47% probability of extinction within 50 years. HMB, LMB, or BURN management slows decline only a small amount relative to no active management and delays extinction by up to about 10 years. Under a scenario with habitat state transition probabilities that more closely project the habitat improvements achieved in the past five years (DINO scenario: black lines), population viability is considerably improved relative to the other four management scenarios, although the metapopulation trajectory still falls below the projection that assumes no change in habitat. All viability metrics for the habitat management scenarios are provided in Supplementary Table S3.

3.4 Sensitivity analyses

3.4.1 Baseline model parameters

The parameter (B) in the logistic function that was used to describe the probability that a helper would disperse from its natal group and attempt to become a breeder was varied from B = 2 (relatively weak dependency on the proportion of Strong habitat that is vacant) to B = 10 (very strong dependency). Within this range, the projections of population size and times to extinction varied relatively little, with slightly better population trajectories when dispersal of helpers to become breeders was more strongly dependent on the availability of Strong habitat. Supplementary Figure S6 shows the comparisons for DINO management. Comparisons across values of B for HMB, LMB, BURN, and NONE management were similar, but with less spread among lines.

The parameter (Pref) in the exponential function that was used to describe the probability that a new breeder would establish a territory in Strong habitat was varied from Pref = 2 (relatively weak dependency on the proportion of vacant potential territories that was Strong habitat) to Pref = 10 (very strong dependency). Within this range, the projections of population size varied relatively little, although median time to extinction was delayed by up to 20 years when the preference for (or accessibility of) Strong habitat was increased. Supplementary Figure S7 shows comparisons for DINO management. Comparisons for HMB, LMB, BURN, and NONE management were similar, but with less spread among lines. Thus, as expected, if new breeders are more likely to establish territories in

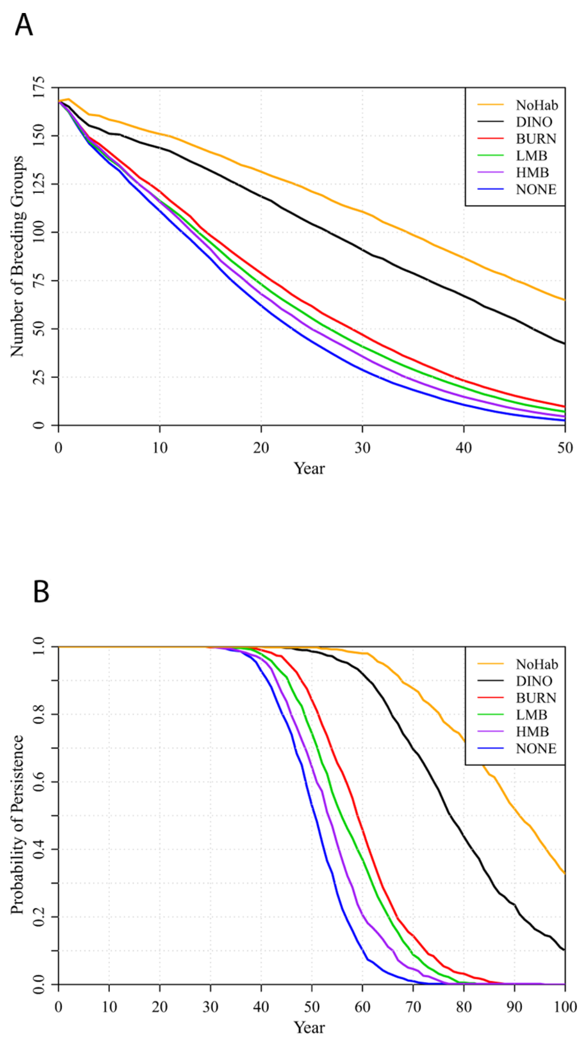

FIGURE 4
Metapopulation projections when habitat change under the several management scenarios is included in the PVA (top to bottom: NoHab, DINO, BURN, LMB, HMB, NONE) **(A)** number of breeding groups and **(B)** probabilities of metapopulation persistence. Probabilities of persistence are graphed through 100 years, because most extinctions occur between 40 and 100 years.

the best available habitat, population viability is improved, although not to an extent that would cause us to question the selection of Pref = 6 in our model.

3.4.2 Inter-population dispersal and connectivity

Population projections and times to extinction under each management scenario are significantly improved if dispersal is more frequent than we initially estimated, or dispersal is increased by expansion of local population boundaries or creation of corridors between populations. Figure 5 shows the effect of 3-fold or 5-fold increase in inter-population dispersal and the projection if the metapopulation is fully interconnected and panmictic for the BURN management scenario. Under panmixia, the metapopulation would consist of 70 occupied territories at 50 years (while the management sustained about 62 Strong, 35 Weak, and 169 Sink potential territories) with 93% probability of persistence through 100 years.

If management can continue to replicate the improvements to habitat that were obtained since 2018 (e.g., with the DINO management scenario), the benefits of increased connectivity are even greater (Figure 6). Under panmixia, the metapopulation would consist of 143 occupied territories at 50 years (while the management sustained about 119 Strong, 36 Weak, and 111 Sink potential territories) with 99% probability of persistence through 100 years. NONE, LMB, and HMB management scenarios also perform better if there is panmixia than otherwise, but they do not sustain the numbers of breeding groups as well as the BURN strategy nor assure metapopulation persistence (Supplementary Figure S8).

3.4.3 Management frequency

Part of the reason that the BURN, LMB, and HMB management regimes do not lead to much better metapopulation viability is because the active management is applied only once per 5 years

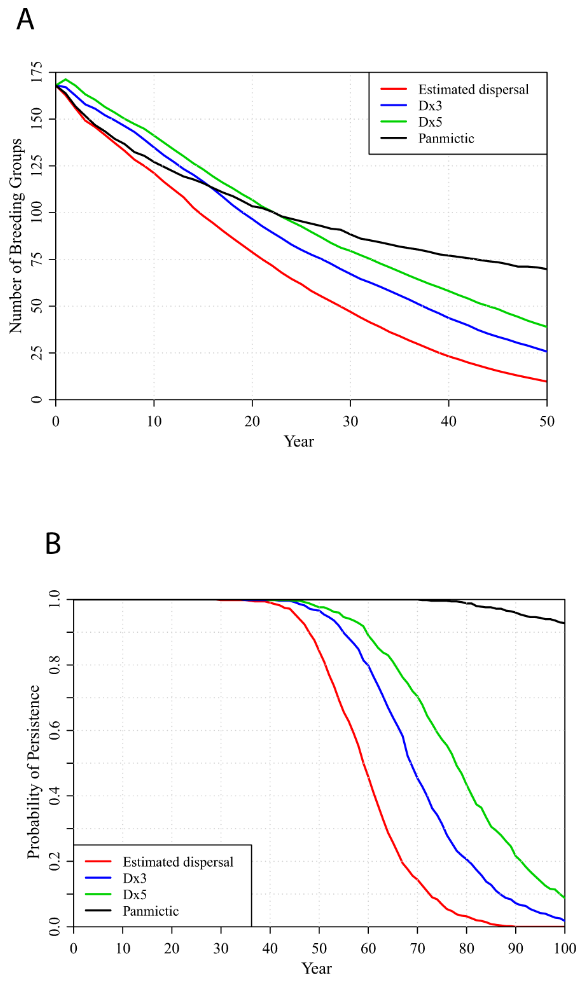

FIGURE 5
Metapopulation projections under the BURN management scenario, with the estimated, 3-fold increase (Dx3 scenario), 5-fold increase (Dx5) inter-population dispersal or complete panmixia (bottom to top): **(A)** number of breeding groups and **(B)** probabilities of metapopulation persistence over 100 years.

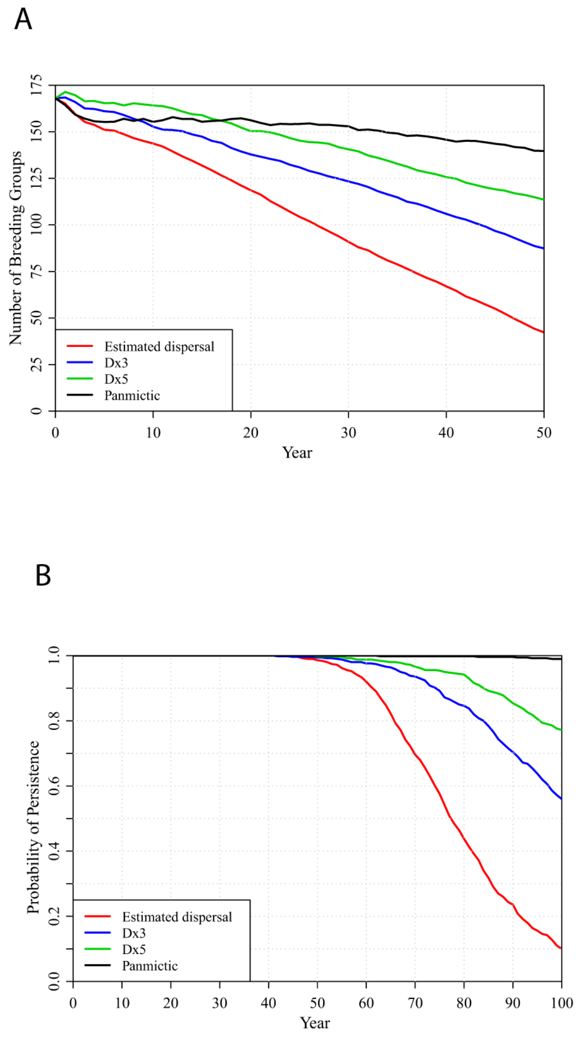

FIGURE 6
Metapopulation projections under the DINO management scenario, with the estimated, 3-fold (Dx3 scenario), 5-fold (Dx5) inter-population dispersal or complete panmixia (bottom to top): **(A)** number of breeding groups and **(B)** probabilities of metapopulation persistence over 100 years.

(with the starting year randomized across local populations), and the other 4 years in each cycle experience habitat state transitions that occur with the NONE management. To test if management might be significantly more successful if it were applied more often to each population, we examined scenarios with each management action applied every 3 years (Figure 7).

Shortening the cycle of active management improves efficacy of the DINO management (top two lines), almost doubling the breeding population at year 50 and increasing the probability of metapopulation persistence for 100 years from 10% to 39%. The improvement in the BURN management (next two lines) was more modest, increasing breeding population at year 50 from 10 to 18 and not avoiding the almost certain extinction within 100 years. LMB (next two lines down) improved population size only from 7 to 11 breeding groups after 50 years and delayed median time to extinction only from 56 to 60 years. A 3-year cycle of HMB (next two lines) provided almost no improvement over the 5-year cycle, and HMB provided only a little better protection for the metapopulation than did no active management (bottom line). Further viability metrics for 5-year and 3-year intervals of habitat management are given in Supplementary Table S3. There was substantial variation among independent iterations of the simulations, as shown by the SDs in Supplementary Table S3, but averaged across the 500 iterations the differences among mean trajectories for different scenarios was consistent.

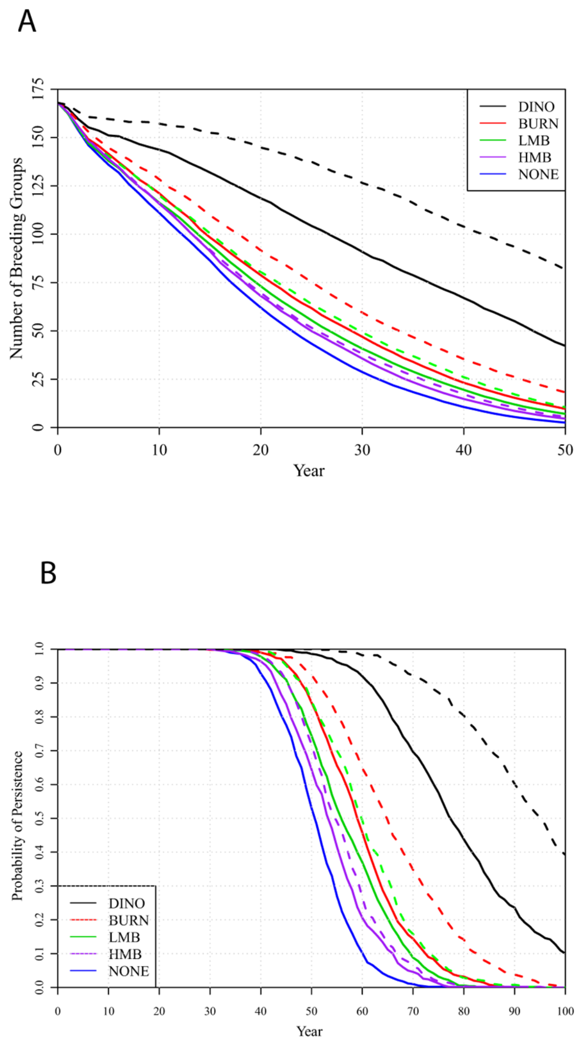

FIGURE 7
Metapopulation projections under each management scenario (top to bottom: DINO, BURN, LMB, HMB), applied every 5 years (solid lines) or every 3 years (dashed lines) or with no active management (bottom line): **(A)** number of breeding groups and **(B)** probabilities of metapopulation persistence over 100 years.

3.5 Population management options

Projections with 3-fold or 5-fold increases in interpopulation dispersal demonstrated the benefits of increased connectivity. Possible options for more direct management of the FSJ populations were therefore coupled with the DINO improved habitat management. The individual options for population management (Connect, Feed, Trans15, and Trans30) were not sufficient to prevent ongoing decline in population size, resulting in a substantial risk of metapopulation extinction within 50 to 100 years (Figure 8, Supplementary Table S4). An increase in the number of breeding pairs that can be accommodated within a given extent of Strong habitat, represented by the Feed option, improved the population relative to not implementing any of the population management options, but inbreeding still accumulates to levels (mean = 0.062, equivalent to first-cousin matings) that would depress first-year survival and thereby result in the metapopulation size eventually falling below most other management options. Connecting the three sets of nearby populations (Connect option) reduces the accumulation of inbreeding and reduces the probability of extinction relative to the Feed option, but results in a similar decline in metapopulation size. Translocating 15 FSJs per year moves almost as many FSJs between populations as occurs with a 3-fold increase in natural dispersal (Trans15: mean = 21.4 scrub-jays move annually via natural dispersal plus the translocations, in the first 5 years before population decline; Dx3: mean = 22.8 move annually), but managed translocations move FSJs selectively from crowded populations to more sparsely occupied ones, rather than moving mostly to adjacent populations as occurs with enhanced natural dispersal, and this results in slower accumulation of inbreeding with managed translocations (Supplementary Table S4). The Trans30 management strategy approaches the benefits projected with 5x dispersal.

Population management options that combine the Feed amplification of Strong territories with translocations were found to nearly stabilize the population size, minimize inbreeding, and with 30 FSJs translocated per year could keep the likelihood of extinction below 10% over 100 years (Figure 9, Supplementary Table S4). Combinations of population management that increase dispersal but do not increase Strong territories (Trans15 + Connect, Trans30 + Connect) result in greater population declines and do not keep the long-term probability of extinction below 10%. Combining all of Feed, Connect, and Translocations can result in population stability and less than 5% probability of extinction (Supplementary Table S4).

4 Discussion

Our updating of prior PVAs reaffirms that the populations of FSJs in the mainland portion of Brevard County, Florida are currently too small and isolated for long-term viability. Moreover, even management of the existing habitat, with the currently low level of connectivity among the set of 14 individually small populations, will not be adequate to prevent further decline and ensure long-term viability. Neither the earlier projections of habitat management options without further manipulation of the population structure (Eaton et al., 2021) nor population management options without further management of the transitional habitat states (Lacy and Breininger, 2021) showed paths forward that would ensure long-term persistence and growth of the metapopulation. A combination of habitat management and direct population management is needed to ensure viability.

The first delisting criterion of the U.S. Fish & Wildlife Service Recovery Plan, that of stable or increasing numbers, can be achieved, but only through a combination of continued aggressive and effective restoration and management of scrub habitat, much greater connectivity among subpopulations, and perhaps also increasing the density of breeding groups through supplemental feeding or other supportive actions. The second criterion, that of maintained genetic diversity, can be achieved at a level of 95% retention over 50 years, but only with increased connectivity that would likely require managed translocations. This would be counter to a requirement for genetic diversity being maintained naturally without translocations. The broadest criterion, that of sustaining habitat sufficient to ensure viability for the foreseeable future, at the level of keeping the likelihood of metapopulation extinction below 5% for 100 years, can be met only if all aspects of habitat and population management are effectively addressed: habitat management that increases optimal scrub habitat; increased connectivity; and further enhancing the sizes of populations that can be sustained in the existing habitat through supplemental feeding or other supportive actions.

Each of these forms of active population management has been shown to be at least plausible biologically and logistically. Translocation is in the early learning stages where family groups or helpers have been moved and translocated individuals often stay in the recipient sites and produce young (Mumme and Below, 1999). Currently all supplemental feeding is unauthorized, but it might increase as conservation sites get more human visitors. Experimental results by Schoech et al. (2008) suggested supplemental feeding might encourage initial FSJ population growth; supplemental feeding has increased populations of other jay species (Derbyshire et al., 2015). Generally, supplemental feeding needs additional research to confirm benefits outweigh risks (Benmazouz et al., 2021).

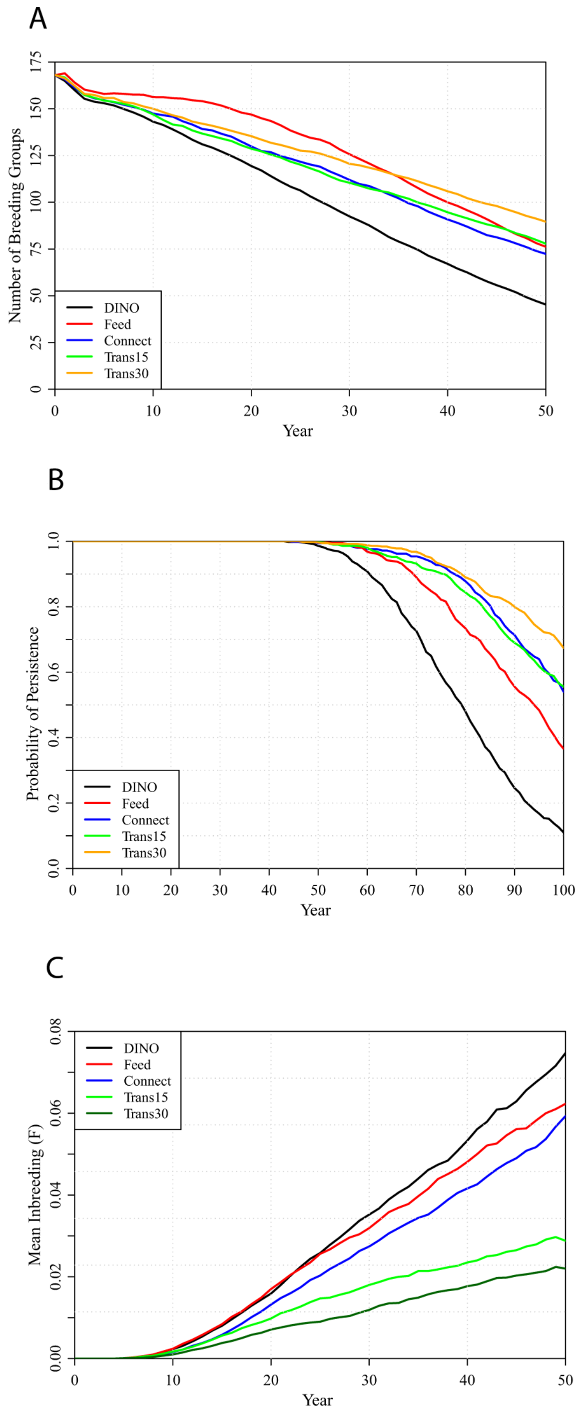

FIGURE 8
Metapopulation projections under several population management scenarios, each applied with DINO habitat management applied every 5 years: DINO habitat management only (bottom line), or with population management connecting 3 sets of adjacent populations (Connect), translocating 15 or 30 FSJs per year (Trans15 and Trans30), or supplemental feeding (Feed). **(A)** number of breeding groups projected over 50 years, **(B)** probabilities of metapopulation persistence over 100 years, and **(C)** inbreeding accumulated over 50 years.

4.1 Improving PVA through links to habitat models

For many species, especially those in transitional habitats, habitat is not static, but PVA itself does not provide the methods for assessing changes to habitat (Akçakaya et al., 2004a, Akçakaya et al., 2005). Habitat characteristics can affect most population processes that are modeled in a PVA: reproduction and survival,

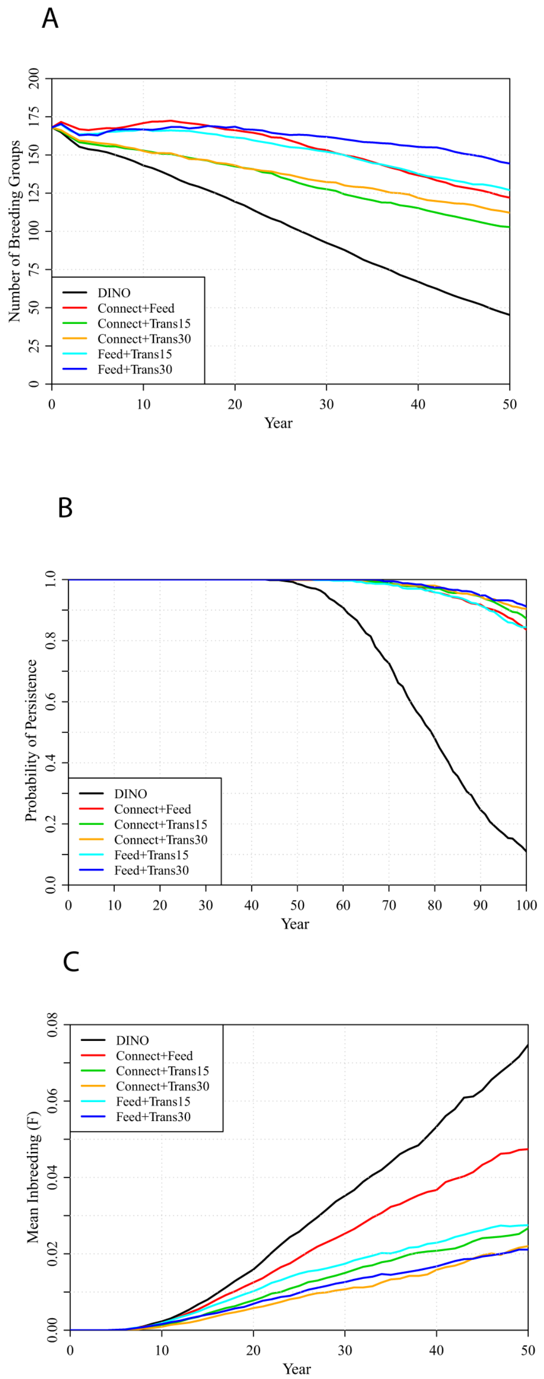

FIGURE 9
Metapopulation projections under several combinations of population management scenarios, each applied with DINO habitat management applied every 5 years: **(A)** number of breeding groups projected over 50 years, **(B)** probabilities of metapopulation persistence over 100 years, and **(C)** inbreeding accumulated over 50 years.

carrying capacity, dispersal, connectivity, and social structure. However, PVAs rarely assess how habitat characteristics drive the vital rates, and rarely do they rely upon quantitative models of habitat change and the functional links of habitat to demographic rates, as conducted herein.

The observed demographic rates for FSJs in Brevard County confirm that the habitat states as classified by the ARM team do have direct impact on reproduction and survival of the FSJs, resulting in positive population growth in the most optimal habitat (OpO), decline in weaker (OpC), and the fastest population decline in habitat with vegetation that is either too short or too tall. The simulations with updated demographic rates confirmed the finding of earlier PVA (Lacy and Breininger, 2021) that isolated populations (or interconnected sets of populations with high rates of exchange) with fewer than about 80 potential territories in OpO habitat are vulnerable to extinction.

Carrying Capacity (K) is a key parameter of most population models, and yet the ecological carrying capacity of an area of habitat for a species is difficult to measure under all environmental conditions. Estimates of K are generally based on estimates of maximum observed prior population densities. However, it is uncommon for PVA models to implement population limitations that explicitly respond to the temporal and spatial variation in habitat quality. Carrying capacity arose in our models by virtue of the source-sink dynamics arising from habitat variability: Strong habitat patches allowed for positive population growth, while the poorer reproduction and survival in Sink habitat resulted in decline. Consequently, carrying capacity emerges from the distribution of habitat and responds to dynamic changes in the habitat. The linkage of habitat projections to population consequences via a mechanism driving carrying capacity in this system is an example of site-dependent population regulation (Kluyver and Tinbergen, 1954; Rodenhouse et al., 1997).

In our modeling, we also included the effect of habitat quality on social structure. We found that metapopulation viability is enhanced by the availability of Strong habitat influencing the likelihood that helper scrub-jays will disperse from natal groups and attempt to establish their own breeding group, and then establishing a territory in best available habitat. However, Sink habitats might play a stabilizing role via providing a buffer that absorbs excess birds when population densities get high, from which new breeders can be readily drawn when vacancies in better habitat arise (Pulliam et al., 1992). Conversely, Sink habitat might drain birds away from optimal habitat, if the tendency for dispersing jays to seek out the best habitat is not strong enough (Lacy and Breininger, 2021; Breininger et al., 2023). Within the ranges of parameter values that we tested, these competing forces apparently largely cancel: populations with a mix of Strong, Weak, and Sink habitat were projected to survive as well as did populations with only the Strong habitat. (E.g., about 80 Strong territories are required for population viability, regardless of whether there are also some Sink territories.) These components of the PVA model illustrate that the effects of dynamic habitat on populations can arise via effects on breeding patterns, dispersal, habitat choice, and likely other population processes that go beyond simple effects on fecundity and survival.

4.2 Effects of incorporating dynamic habitat projections into the PVA

The PVA model presented in Lacy and Breininger (2021) was a highly detailed, individual-based model that included components of population dynamics that are often ignored in simpler PVAs. Even with the inclusion of such complexity in the PVA, we now find that it makes a big difference to the PVA projections if we assume (as is done in many PVAs) that the current state of the habitat and the consequent demographic rates will persist (the "NoHab" scenarios that repeated the assumptions made in the prior PVA) vs projecting the habitat dynamics and the impacts on the population. The earlier PVA results were apparently too optimistic, in that they did not account for the expected transition of optimal oak scrub habitat to Tall and Tall-Mixed pine and oak woodland in the absence of very aggressive and ongoing management to regenerate scrub.

The pessimistic projections of population viability under prior levels of management helped to drive efforts to use much more aggressive management to restore optimal habitat. The DINO improvements to habitat suggest that managers can have greater control over habitat quality than previously considered using range-wide plant community management strategies relying mostly on fire alone as a management tool. Previous mechanical cutting methods relied on taking the tallest vegetation to the ground with hopes that fire thereafter could maintain the system, but this has not succeeded. Fires are difficult to start and then control, and cutting oaks to the ground results in dense sprouting vegetation that often burns poorly and results in few openings jays need. These early mechanical treatments were focused on the most degraded habitat, possibly explaining why they had worse results than fire alone and suggesting the need for continued innovation. Florida scrub-jay habitat quality is often considered an indicator of conditions for many unique plants and animals in scrub, and innovations for FSJs will need to be tested for other species of conservation concern that require frequent fire and also now reside in fragmented habitat (Kent and Kindell, 2010).

4.3 Management implications

Given the uncertainties in the habitat transition probabilities for different management regimes, this study should be seen as a presentation of a methodology and a demonstration of the potentially large impact on PVA results when projections of habitat change are included and integrated with the population model. Even so, the general trends revealed provide some guidance as to what management is necessary to sustain a viable metapopulation of FSJs in Brevard County.

The combined habitat and population modeling indicate that achieving the recovery goals of long-term stability, metapopulation persistence, and retaining adequate genetic diversity will require a combination of management of the scrub habitat, improving the capacity of even the optimal habitat to support breeding groups, and increasing connectivity among local populations. Attending to just one or two of these proposed actions, as might be suggested by a strictly habitat analysis or a strictly population analysis, will not be adequate. The recent history of success in restoring optimal scrub via mechanical removal of trees was represented by the DINO scenarios in our model, but the actual habitat transition probabilities will need to be monitored over time. Increased connectivity of local populations might be achieved by a combination of the means tested in our model: improving corridors that would allow for functional merging of some sets of local populations, actions that increase rate of inter-population dispersal through improved habitat management, or managed translocations. Given the importance of increasing connectivity, it will be important to monitor the effectiveness of whatever means are selected, either through tracking of movements of individual FSJs or through genetic monitoring to assess the consequences of increase connectivity or, ideally, both. The need also to manage for a higher density of breeding groups to be supported within available habitat might be achieved by supplemental feeding or other means to further improve the demographic performance of FSJs in each habitat state.

Our habitat-PVA model can provide the basis for testing more specific options for management, including determining: the number of optimal territories needed for a local population to provide benefit to the metapopulation, the necessary interval in years between habitat restoration actions, the schedule of translocations and best age classes and social composition to be moved, the number of exchanges of FSJs required for adjacent populations to function as fully connected units, the effect on the metapopulation of the loss of any of the populations, and the rate at which FSJs can be removed from healthy local populations to be used to reinforce or reestablish other populations or metapopulations.

4.4 Limitations and further needs

Adequately understanding the processes that threaten the viability of the FSJ metapopulation and the consequences of various proposed management actions required detailed data on population structure and demography, understanding of the relationships between demographic rates and habitat characteristics, knowledge of the behavioral responses to habitat quality and availability, habitat models for estimating projected changes in habitat quality, and comprehensive models for integrating habitat and population processes. For the FSJ such data have been generated over decades of extensive monitoring and research of both the Brevard County metapopulations and the metapopulation at Archbold Biological Station in south-central Florida (Woolfenden and Fitzpatrick, 1984; Fitzpatrick and Bowman, 2016). For many other species requiring habitat and population management, such data are not available and mechanistic models as detailed and complex as those we present would not be possible. Instead, PVA might be restricted to predictions of occupancy rates and mean growth rates, each based on empirical trends rather than on demographic modeling to generate those trends in mechanistic simulations (Nichols et al., 2024). Similarly, the modeling of habitat transitions might be limited to a dichotomous switching between suitable and unsuitable states or, conversely, might be based on a more mechanistic understanding of the factors driving habitat change that provides more refined projections than did our use of estimated transition probabilities.

The current and potential future values for many of the variables in our models are uncertain, so specific predictions might be overly optimistic or pessimistic. Extensive sensitivity analysis of key model parameters (e.g., natural dispersal rates, annual variability in demographic rates, effects of inbreeding) was provided in Lacy and Breininger (2021) and those analyses indicate that the general trends described above are sufficiently robust to parameter uncertainty. However, structural (process) uncertainty about the driving processes and the functional relationships is harder to assess because, by definition, it is the limitations in our knowledge about how the system works and what kinds of models can adequately represent it. Further exploration could omit or add component processes (habitat, demographic, social, or genetic) to the Vortex model that we used, in order to determine if our understanding of the system changes. In addition, alternative models of the habitat dynamics, such as can be done with the ST-Sim package for spatially explicit modeling of vegetation change (Daniel et al., 2016; docs.stsim.net), and for population dynamics, such as the HexSim spatially explicit, individual-based PVA (Schumaker and Brookes, 2018; hexsim.net), could be explored and predictions compared to those that we obtained with Vortex. Other available approaches include linking population models to Landis landscape models (Akçakaya et al., 2004b; Akçakaya et al., 2005).

We linked habitat and population models by including habitat transition probabilities that had been developed in the ARM project into macros that specified within the Vortex PVA the changing numbers of potential territories in each habitat state. Although we implemented the habitat transitions as probabilistic events, we did not include uncertainty in the transition probabilities in our modeling. Measures of uncertainty in the habitat transitions could be implemented within the macros by sampling the transition probabilities from distributions that describe their uncertainties. Another source of uncertainty that we were not able to include in our analyses is management uncertainty – the variability in application of and results from management actions that are recommended. We assumed that the management regimes we tested would be applied uniformly across the 14 local populations of the metapopulation, with the same consequences for the habitat. More complex models of habitat change might include additional habitat states or modifying characteristics, dependencies on spatial arrangement of habitat, or dependencies on the history of states rather than just the immediately prior habitat state. Such processes might need to be represented in a habitat model that is more complex than could be described in the simple macro language available within Vortex. The lack of certainty about both process (model structure) and parameter values, and the possibility that new methods of habitat and population management might be envisioned and tested, means that habitat and population responses to environmental change and management actions will need to be monitored, and data and models regularly updated, to allow for adaptive management of this threatened species.

Even if all the model parameters were correctly estimated, both the habitat transitions and the FSJ population dynamics include many stochastic processes, and consequently there was large variation among the iterations of any given scenario (see Figure 2 and Supplementary Tables S3, S4). Thus, although monitoring the fate of the habitat and populations will be an essential component of the adaptive management (Nichols et al., 2024), researchers and managers will need to recognize that the outcomes over just a few years of management might by chance be considerably better or worse than the expectation for the system. Well-informed management can increase the probability of success, but not guarantee it.

For some species, the wildlife population might impact its habitat in important ways, so that the habitat transitions are influenced by the population trajectory as well as the reverse. To capture these interactive dynamics between the population and its habitat might require that the habitat transition probabilities and the population changes be modeled simultaneously or interleaved on an annual or other timestep basis. This could be achieved by including in the Vortex scenario calls each simulation year to an external program written in R (R Core Team, 2020) that simulates habitat transitions based on the current state of both habitat and the population (and possibly other external drivers). Alternatively, a "metamodel" (Lacy et al., 2013) that includes both a model for estimating habitat transitions and a population model could step through both the habitat transition and population response one iteration and one year at a time.

Each level of complexity added to the linked analysis of habitat and population will increase potential for error in modeling the system or estimating parameters. Moreover, added complexity can make the causes of emergent trends more difficult to discern and to present to decision-makers, possibly without adding significant increase in accuracy of projections. Therefore, it will be important to determine how much realism is needed to capture the system dynamics adequately to guide successful management.

4.5 Value of integrated habitat and population modelling

Despite uncertainties, attempts at modeling such complexities bring together multidisciplinary collaborations (e.g., field and population ecologists, geneticists, land managers, and conservation land acquisition specialists) that learn to communicate more clearly with one another, reducing jargon and misunderstanding about geographical scale and time horizons. For this metapopulation of Florida scrub-jays, multi-disciplinary collaboration and integrated use of multiple modelling systems helped lead to recognition of the failure of past management practices to ensure long-term persistence, experimentation with new ways to manage both the scrub habitat and the FSJ populations, and identification of combinations of actions that are projected to result in population persistence and recovery.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Zenodo repository: 10.5281/zenodo.13850866.

Author contributions

RL: Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. DRB: Conceptualization, Data curation, Investigation, Project administration, Writing – review & editing. DJB: Data curation, Formal analysis, Writing – review & editing. AS: Investigation, Writing – review & editing. AF: Investigation, Writing – review & editing. EH: Investigation, Writing – review & editing. SM: Investigation, Resources, Writing – review & editing. DD: Investigation, Resources, Writing – review & editing. TM: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Securing black lion tamarin populations: improving habitat-based inputs and risks for population viability analysis to inform management decisions

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Wild populations across the globe face an escalating risk of decline and potential extinction due to a variety of threats. Key among these are habitat loss and degradation, which results in smaller, isolated populations that are vulnerable to stochastic effects. The Endangered black lion tamarin (*Leontopithecus chrysopygus*) survives in 17 fragments of the Atlantic Forest within the Paranapanema River basin, in southeast Brazil, with an estimated 2,255 individuals. Life history and threat data from the 2005 Population Viability Analysis (PVA) for this species were updated and augmented, including new estimates of environmental resistance factors present in, or projected for, their habitat. Notably, improved estimates of carrying capacity for this species were developed using a plant-based energetic model. Climate change and fire risk data were incorporated to project future carrying capacity, and habitat connectivity supported estimates of black lion tamarin dispersal across this fragmented landscape. The resulting population viability projections using Vortex simulation software identify core subpopulations with low extinction risk and high gene diversity, as well as smaller subpopulations with low long-term viability, highlighting the need for targeted conservation strategies across the fragmented metapopulation.

KEYWORDS

carrying capacity, climate change, fire risk, vortex, metapopulation, conservation planning

1 Introduction

Wild populations are at risk of decline or even extinction due to many threats, including habitat loss or degradation that can fragment populations. Small, isolated populations are impacted more significantly by the synergistic impacts of stochastic processes. As a result, ecological, demographic, and genetic population consequences may interact in a feedback loop, leading the species into an extinction vortex (Gilpin and Soulé, 1986). To assess these risks for the black lion tamarin (*Leontopithecus chrysopygus*), categorized as Endangered (EN) on both the IUCN Red List (Rezende et al., 2020) and the Brazilian national assessment (Brasil, Ministério do Meio Ambiente (MMA), 2022), a Population Viability Analysis (PVA) was completed in 2005 (Holst et al., 2006) using the best available data for lion tamarin species and expert opinion. Interdisciplinary actions have been implemented from the resulting Action Plan and the subsequent Brazilian National Actions Plans (NAP) developed for this species. Since 2005, this PVA has guided the conservation of the species and informed decisions regarding habitat management and conservation actions, with the management goal of retaining >98% gene diversity and having <2% probability of extinction for 100 years. However, with accumulated results from various research and conservation activities, including the emergence of new knowledge about additional populations and threats affecting both habitat and wild populations, the need for an updated PVA became essential to re-evaluate projected viability and needed management actions. The aim of this modeling effort was to update the black lion tamarin PVA by incorporating the most current population information and to improve the model parameters by incorporating habitat-based data and risks imposed by fire and climate change. This will provide an improved tool for future conservation planning by managers and other stakeholders. We also explored the importance of connectivity across this fragmented landscape for this species to help guide management efforts.

Wild populations of the black lion tamarin (BLT) are currently present in 17 locations within the Atlantic Forest in the Paranapanema River basin, in the state of São Paulo, in southeast Brazil. These locations were historically connected; therefore, for management purposes, the populations that live there fall under the concept of metapopulation and will be treated here as subpopulations, subject to a dynamic of interdependence. These subpopulations were modeled using Vortex software v10.4 (Lacy and Pollak, 2020), a Monte Carlo individual-based simulation that can incorporate both stochastic and deterministic processes on demography and genetics (Lacy, 1993, 2000a, 2000b; Lacy et al., 2019; Lacy, 2019). Vortex is well suited to model the life history and stochastic processes of small vertebrate populations such as the BLT metapopulation.

The value and appropriate use of PVA projections is directly related to the quality of data used to estimate model parameter inputs, including demogaphic rates, population status, genetics, and projected threats. Habitat carrying capacity (K) for the target species can be a crucial model parameter, as it places a limit on population size that, in turn, affects population viability, and also affects density-dependent demographic rates. However, this parameter can be among the most challenging to estimate.

The relationship between wild BLT subpopulations and the conditions and characteristics of the vegetation cover and habitat (*i.e.*, the environmental resistance) are key, as these define the habitat carrying capacity for the species and affect demographic rates. Consequently, for this PVA we sought to improve estimates of current habitat carrying capacity and BLT subpopulation sizes based on an energetics model study. Additional data sources were used to project future carrying capacity for BLTs based on projections of climate change effects and estimated fire risk, accounting for the regeneration and recovery capacity of the vegetation in affected areas. Projected progressive increases in suitable BLT habitat due to restoration efforts underway in the ecological cores of the Pontal do Paranapanema region – the subbasin at the mouth of the Paranapanema River – were considered in estimating future dispersal patterns of the species. We offer this as an example of how to incorporate data and methodology from other research into PVA to improve its effectiveness for evaluating conservation needs and actions. By incorporating additional data (*e.g.*, updated population census), knowledge (*e.g.*, new subpopulations), parameterization tools (*e.g.*, plant-based energetics model to estimate K), and risk factors (*e.g.*, habitat-based estimation of fire risk, projected climate change impacts), we endeavor to develop a more current and comprehensive model that can support future conservation decision making for this species. The resulting model also enables us to assess the relative importance that connectivity may play in population viability.

2 Materials and methods

2.1 Species distribution

The area of this study corresponds to the Atlantic Forest fragments of the current BLT occurrence (Figure 1), within the hydrological basin of the Paranapanema River (Garbino et al., 2016) that can be considered as three regions for BLTs. About 60% of the BLT wild population lives in western state of São Paulo, a region called Pontal do Paranapanema (Pontal metapopulation), divided in four fragments: the Morro do Diabo State Park, two private fragments, and the Black Lion Tamarin Ecological Station (Holst et al., 2006; Garbino et al., 2016). In the center-east of the state, the Médio Paranapanema region (Médio metapopulation), are the two subpopulations of Caetetus Ecological Station and Fazenda Rio Claro/Turvinho, and a reintroduced population in Mosquito Private Natural Heritage Reserve (RPPN in Portuguese, acronym for Reserva Particular do Patrimônio Natural). In south-eastern São Paulo, the Alto Paranapanema region (Alto metapopulation), the species occurs in fragments in Guareí, Buri, Itapeva, Paranapanema, Taquarivaí and Angatuba municipalities (Culot et al., 2015; Lima et al., 2003). A recent record of BLT groups in the Paranaciacaba Mountain chain, in the municipalities of Pilar do Sul and São Miguel Arcanjo, could significantly influence the population dynamics and conservation status of the species (Röhe et al., 2003; Rodrigues et al., 2016).

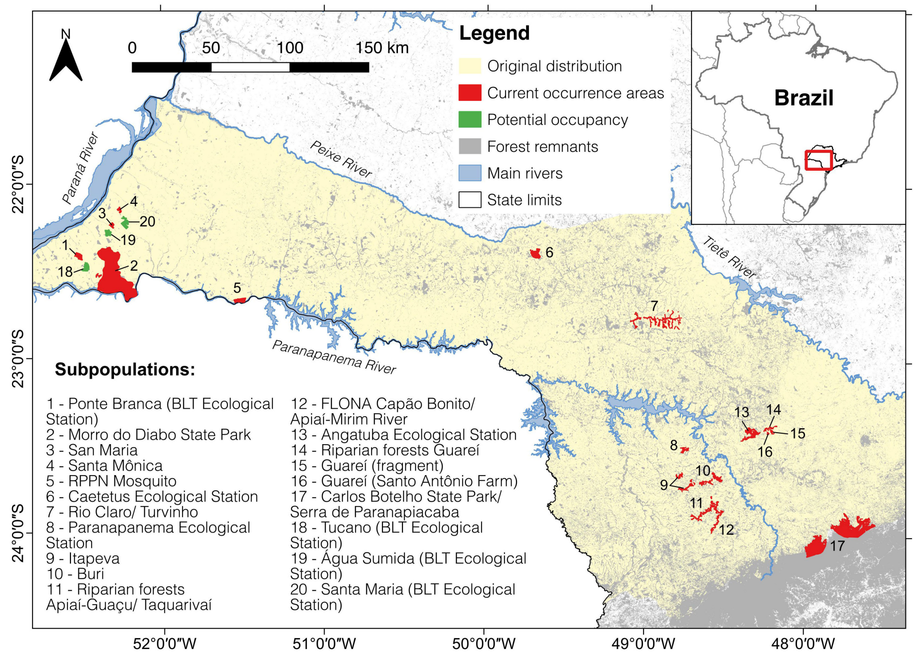

FIGURE 1
Black lion tamarin distribution map showing each of the 17 known subpopulations for the species (red) and the possible occupancy areas (green) considered in this study. Each subpopulation is numbered and named. Data source: IPÊ, Institute for Ecological Research.

2.2 Species habitat needs

Black lion tamarins belong to the family Callitrichidae, the smallest primates in the Neotropics, are diurnal, and live in family groups of usually two to eight individuals (Coimbra-Filho and Mittermeier, 1977). They have frugivorous-insectivorous diets, but consume other food items like nectar, exudates (gum and sap), and small vertebrates (Valladares-Pádua, 1993; Passos, 1999). BLTs consume at least 53 fruit species across 24 families; consumed fruits are typically small, soft, sweet, and with a lot of pulp, and are collected more from trees than from vines or lianas, most of which belong to the Myrtaceae family (Valladares-Pádua, 1993). One of the most frequently eaten fruits throughout the year, *Syagrus romanzoffiana* (Arecaceae), has been identified as the most important resource in many areas where BLTs occur, as it is available throughout the dry season when most other fruits are not (Valladares-Pádua, 1993; Mamede-Costa and Gobbi, 1998). The consumption of tree exudates comprised 0 to 55% of the observations, mainly during the dry season (Passos, 1999). Foraging occurs in natural hollows of trees, bark, palm fronds and sheaths of fronds, flowers, and other similar places (Valladares-Pádua, 1993; Passos, 1999). Tree hollows are the predominant places for night shelter, and all these sites belong to or are close to areas of intensive use by the groups (Valladares-Pádua, 1993). The BLT occupancy areas total ~480 km^2 (Valladares-Pádua, 1993; Baker et al., 2002), and the number of individuals in the wild was estimated at 1,500 in 2005 (Paranhos, 2006; Holst et al., 2006).

2.3 Population simulation model

The Vortex simulation program tracks an age- and sex-structured population, stepping each individual through a series of life events (reproduction, survival, inter-population dispersal) for each time step (typically one year). Age- and sex-specific demographic rates are entered as means that represent probabilities and are applied by generating a random number from 0 to 1 for each individual and event to determine the stochastic result (*e.g.*, survival or death; breed or not breed), a process that inherently incorporates demographic stochasticity into the results. Means can be entered as a fixed value or as a distribution to incorporate parametric uncertainty. Year-to-year environmental variation (EV) is inputted as a standard deviation around the mean rate to create a binomial distribution used for the entire iteration, from which the year-specific mean rate to be used for all individuals in a given year is selected. Catastrophes are treated as outlier events with a specified annual risk of occurrence (by generating a random number from 0 to 1 at the beginning of each year and comparing it to the specified annual probability of occurrence) that can be specified to affect survival (*e.g.*, disease), reproduction and/or carrying capacity (*e.g.*, fire). Initial individuals are given two unique alleles at one neutral locus to track genetic diversity through a gene drop process, while kinships are used to track individual inbreeding coefficients. Inbreeding depression can be applied through recessive lethal alleles and/or decreased survival of inbred individuals (see Supplementary Material and Lacy et al., 2019 for further details on Vortex model structure and processes).

Life history model inputs were taken from the 2005 PVA black lion tamarin model (Holst et al., 2006), which was based upon the best available field data for lion tamarin species and opinion of species experts at that time. Baseline life history data were taken primarily from a 21-year dataset for wild golden lion tamarins (*L. rosalia*) by Baker and Dietz (Baker and Dietz, 1996; Baker et al., 1993, 2002; Dietz and Baker, 1993; Dietz and Baker, unpublished data; Dietz et al., 1997) and used to calculate reproductive and survival parameters, mating system, inbreeding effects, environmental variation, and density-dependent predation effects (Holst et al., 2006). These inputs are generally described below and more fully in the Supplementary Material (Supplementary Table 1 and accompanying text) and Holst et al. (2006).

A base scenario was developed with the best available estimates for BLT demographic rates and inbreeding sensitivity (Supplementary Table 1) but with no catastrophes or habitat loss. Sensitivity testing scenarios were developed using populations of 500 individuals (N_0=K=500) and varying inputs by +/-10% of the base value, where appropriate (calculated on survival, not mortality) to assess the sensitivity of model results to these model inputs. For age-based inputs (*e.g.*, first age of reproduction), which must be entered as integers, we tested ages within 1-2 years of the base value that were biologically plausible. The Current scenario represents the current BLT metapopulation and habitat estimates, incorporates additional threats (catastrophes and habitat loss due to climate change), and represents the best available estimates for current and future conditions to project future viability of BLT subpopulations and metapopulation (Supplementary Table 1). Additional scenarios (Isolated) were developed by removing all connectivity between subpopulations from the Current scenario. Each scenario was run (1000 iterations) for 100 years (starting in 2020); this represents approximately 14 generations for this species (Baker et al., 2002 *apud* Kleiman and Rylands, 2008; Rezende et al., 2020) and is sufficient to observe instabilities in populations and long-term population trends (Lacy et al., 2019). Model outputs included mean and standard deviation for population size (N), gene diversity (GD, *i.e.*, expected heterozygosity based on a single neutral locus), and stochastic growth (r), as well as estimated extinction risk (PE), for each subpopulation and for combined subpopulations within each region, over the 100-year projections. In this model, extinction is defined as the absence of at least one sex.

2.4 Species-based model inputs

Although field and genetic data show that lion tamarins are not entirely monogamous (Baker et al., 2002 *apud* Kleiman and Rylands, 2008; Garcia et al., 2021; P. D. Freitas, personal communication), long-term monogamy represents the best description of the mating system of the species (Holst et al., 2006). Reproductive lifespan was set at age 4-13 years for females and 4-16 years for males (Holst et al., 2006). Data for wild lion tamarins tracked in the studbook indicate that few animals survive beyond 16 years (Valladares-Pádua, 1993; Baker et al., 2002; Holst et al., 2006). Captive studbook data suggest that females may become post-reproductive at age 13, while males remain reproducing throughout their lives.

The mean percent of adult females breeding in a given year was set at 73% (with 9.4% EV as a standard deviation), based on a 21-year dataset of wild golden lion tamarins (Baker et al., 2002) and used in the 2005 PVA (Holst et al., 2006). Of those adult females that breed in a given year, reproduction was limited to a maximum of two litters per breeding pair per year, with a maximum of two offspring per litter (at equal sex ratio). Reproduction was not considered to be density-dependent. Mean number of offspring (births) per pair per year was estimated by applying the observed ratio from captive litter size/mean # offspring per year in the wild for golden lion tamarins (1.9/2.14) and applying this to captive BLT mean litter size (1.76). The resulting average of 1.99 offspring per year was applied to reproducing pairs, as follows: 82.5% (1 litter) and 17.5% (2 litters), with one (31%) or two (69%) offspring. These percentages were applied stochastically by drawing a random number from 0 to 1 for each female that breeds in a given year to determine the number of litters she produces that year, and then drawing another random number for each litter to determine if 1 or 2 offspring are born in that litter.

Age- and sex-specific mortality rates were taken from the 2005 PVA (see Supplementary Table 1). While we recognize that mortality causes may differ between protected and non-protected areas, there is no evidence that mortality rates are different. Mortality rates were modelled as density-dependent, increasing when N is over 50% of the habitat's carrying capacity (K, *i.e.*, the upper limit of BLT population size for that habitat). This was estimated by classifying a greater percentage of observed disappearances of individuals in the field as mortality events as density increases, as species experts agree it is unlikely such individuals successfully found vacancies, especially at high density (see Supplementary Material and Holst et al., 2006 for details). These demographic rates result in a deterministic growth rate of $r = 0.1074$ at low densities ($N < 50\%$ K) and $r = 0.0461$ at saturation ($N = K$), prior to the influence of stochastic processes that lower observed growth. Additional mortality is applied in the model via truncation to carrying capacity at the end of each year if N exceeds K, which brings final population growth to approximately zero when the population is at capacity.

The reduction in fitness in inbred individuals is known as inbreeding depression and can be estimated using the function $S=S_0e^{-bF}$, where S_0 is the survival of non-inbred individuals, F is the inbreeding coefficient, b is the average number of lethal alleles per haploid genome, and S is the resulting survival rate (Morton et al., 1956). The value b is a measure of the severity of inbreeding effects through both lethal and non-lethal mechanisms. For diploid species, $2b$ represents the number of "lethal equivalents" that account for inbreeding impacts (see Supplementary Material for details). Inbreeding impacts were modeled as 4.07 lethal equivalents (LEs) applied to first-year survival and 4 LEs to sub-adult survival. These estimates represent the best available data for wild lion tamarins and were based on pedigree data from wild golden lion tamarin populations and used in previous PVA models for other lion tamarin species (Ballou et al., 1998; Holst et al., 2006). The combined value of 8.07 LEs represents 65% of the average impacts estimated for wild vertebrate populations (O'Grady et al., 2006) and are considered by species experts to be a reasonable, conservative estimate for lion tamarins.

Small BLT subpopulations with fewer than 50 individuals (1-Ponte Branca/BLT Ecological Station, 3-San Maria, 4-Santa Monica, 5-RPPN Mosquito, 6-Caetetus Ecological Station 8-Paranapanema Ecological Station, 13-Angatuba Ecological Station, 14-Riparian forests Guareí, 15-Guareí/fragment, and 16-Guareí/Santo Antônio Farm; see Table 1 for population sizes) are believed to have been isolated for at least 10-20 years, with the current individuals more likely to be related to each other than in the larger subpopulations. To account for this, both initial kinships and individual inbreeding coefficients in these small subpopulations were set to 0.01 based on modeling of inbreeding accumulation in similarly sized hypothetical BLT subpopulations (~ mean inbreeding after 10-15 years). Results for mean gene diversity (GD) and mean inbreeding (F) were calculated based on these kinships instead of on allele frequencies (software default option).

2.5 Habitat-based model inputs

2.5.1 Fragment identification

Seventeen habitat fragments harboring BLTs were identified (Figure 1, population numbers 1-17), as well as three additional adjacent habitat fragments with no records of BLT presence but in the process of being connected to BLT-occupied habitat through forest corridor restoration (Figure 1, population numbers 18-20). These 17 occupied fragments and 3 empty fragments are located in three sub-watersheds of Paranapanema river basin, here called regions: Pontal (1-2-3-4-18-19-20); Medio (5-6-7); and Alto (8-9-10-11-12-13-14-15-16-17). These fragments, and the size of each fragment, were defined as follows:

a. If the fragment is a Brazilian protected area, the official size was used. Fragments: 1-Ponte Branca (BLT Ecological Station); 5-RPPN Mosquito; 6-Caetetus Ecological Station; 8-Paranapanema Ecological Station; 13-Angatuba Ecological Station; 18-Tucano (BLT Ecological Station); 19-Água Sumida (BLT Ecological Station); 20-Santa Maria (BLT Ecological Station).
b. If BLT fieldwork has been carried out within a fragment, the areas identified as suitable habitat for the species were used as a baseline and summed to adjacent (connected) areas given by the MapBiomas database of forest remnants (Souza et al., 2020). Fragments: 2-Morro do Diabo State Park; 7-Rio Claro/Turvinho; 12-Capão Bonito National Forest (FLONA)/Apiaí-Mirim River.
c. If no information exists on fragment size, the MapBiomas database of forest remnants (Souza et al., 2020) was used to estimate the areas occupied by BLTs. Fragments: 3-San Maria; 4-Santa Mônica; 9-Itapeva; 10-Buri; 11-Riparian forests Apiaí-Guaçu/Taquarivaí; 14-Riparian forests Guareí; 15-Guareí (fragment); 16-Guareí (Santo Antônio Farm).
d. For the population of the Carlos Botelho State Park/Serra de Paranapiacaba, where the species occupancy is unknown, a buffer zone was estimated between the two occurrence records (32 km apart) within this continuous forest. Fragment: 17-Serra de Paranaciacaba (Carlos Botelho State Park and João XXIII).

2.5.2 Population size estimates

The starting BLT population size for each of the 17 occupied habitat fragments (see corresponding numbers in Figure 1) was derived as follows:

a. If a population density study was carried out, the available information was used. Fragments: 2-Morro do Diabo State Park (Paranhos, 2006), 4-Santa Mônica (Culot et al., 2018), 5-RPPN Mosquito (Culot et al., 2018), 6-Caetetus Ecological Station (Passos, 1999), 7-Rio Claro/Turvinho (Mamede-Costa, 1997), 12-FLONA Capão Bonito/Apiaí-Mirim River (Caldano, 2014), 13-Angatuba Ecological Station (Culot et al., 2018), 14-Riparian forests Guareí, 15-Guareí/fragment, 16-Guareí/Santo Antônio Farm (Pinto, 2017).
b. If population density study was not conducted, but the fragment was in close proximity to one where this information is known and has similar characteristics (size, successional state, vegetation type, and potential connectivity), the density value was extrapolated with high or low confidence, according to the available knowledge from fieldwork activities in those areas. Fragments: 1-Ponte Branca/BLT Ecological Station and 3-San Maria (2-Morro do Diabo State Park values), 11-Riparian forests Apiaí-Guaçu/Taquarivaí, 10-Buri and 9-Itapeva (12-FLONA Capão Bonito/Apiaí-Mirim River values).
c. If there are no studies and the fragment characteristics are unknown, the lowest population density recorded for the species was used to estimate population size (Ruiz-Miranda et al., 2019), in this case, 0.01 individuals/ha (Passos, 1999). Fragments: 17-Carlos Botelho State Park/Serra de Paranapiacaba.

Because of the uncertainty in the current population size for each subpopulation, it was decided to start each simulation with an initial population size drawn from a shifted and scaled beta distribution defined by the minimum, maximum, and the best estimate of the current N for each of the 17 subpopulations (Table 1). In technical terms, for each population we changed the support of the beta function beta($x;\alpha,\beta$) from $x\in[0,1]$ to $y\in[\text{Min N}, \text{Max N}]$ and adjusted α and β so that the mode of beta($y;\alpha,\beta$) is equivalent to the Estimate of current N (with Min N, Max N, and Estimate of current N according to Table 1). This incorporates our uncertainty in the current number of BLTs in each subpopulation. Draws from this composed beta distribution (10,000 iterations) result in a right-skewed distribution of the current number of black lion tamarins

TABLE 1 Initial population size (N) of the 17 subpopulations of black lion tamarin.

#	Subpopulation	Hectares	Estimate of current N	Min N	Max N
1	Ponte Branca (BLT Ecological Station)	1,306	46	37	55
2	Morro do Diabo State Park	32,641	1,142	914	1,370
3	San Maria	515	18	14	22
4	Santa Mônica	484	3	2	17
5	RPPN Mosquito	1,534	14	11	17
6	ESEC Caetetus	2,254	23	18	74
7	Rio Claro/Turvinho	1,799	83	66	100
8	Paranapanema Ecological Station	635	6	5	21
9	Itapeva	1,947	64	51	175
10	Buri	2,986	99	79	269
11	Riparian forests Apiaí-Guaçu/Taquarivaí	2,831	277	93	332
12	FLONA Capão Bonito/Apiaí-Mirim River	754	74	25	89
13	Angatuba Ecological Station	1,394	46	37	137
14	Riparian forests Guareí	83	12	10	14
15	Guareí (fragment)	105	15	12	18
16	Guareí (Santo Antônio Farm)	96	13	10	16
17	Carlos Botelho State Park/Serra de Paranapiacaba	32,000	320	256	1,056
	TOTAL	**83,364**	**2,255**		

Total hectares and population estimate in bold.

in the wild, ranging from approximately 2,000 to 3,100, with a mode of 2,255 and a mean of 2,453 (SD = ± 186). This value may be overestimated, due to the extrapolation of the population density for Carlos Botelho State Park/Serra de Paranapiacaba, whose occupied area is completely unknown, but since it is an extensive continuous forest, its estimated population size raised the total population by at least 256 individuals (based on Min N; Table 1).

Distribution of initial individuals into age and sex classes followed an estimated stable age distribution by Vortex based on demographic rates when N/K = 0.75. All initial individuals were assumed to be unrelated (kinships = 0) except for small subpopulations as described above under Species-based Model Inputs.

2.5.3 Connectivity

While the wild BLT metapopulation is fragmented, some habitat connectivity is estimated to exist among some of these fragments, due in part to habitat corridor restoration efforts or to existing riparian forests. To estimate long-distance dispersal rates, information on the use of the habitat matrix by the species (Pinto, 2017; Santos, 2016) and the current state of the landscape connectivity were considered, as these factors directly influence the dispersion of individuals between one subpopulation and another. Four sets of habitat fragments with potential connectivity were identified, falling in the Pontal and Alto regions: Fragments 1-Ponte Branca (BLT Ecological Station)/2-Morro do Diabo State Park/18-Tucano (BLT Ecological Station); fragments 3-San Maria/4-Santa Mônica/19-Água Sumida (BLT Ecological Station)/20-Santa Maria (BLT Ecological Station); fragments 8-Paranapanema Ecological Station/9-Itapeva/10-Buri/11-Riparian forests Apiaí-Guaçu/Taquarivaí/12-FLONA Capão Bonito/Apiaí-Mirim River; and fragments 13-Angatuba Ecological Station/14-Riparian forests Guareí/15-Guareí (fragment)/16-Guareí (Santo Antônio farm). For connected fragments, the rate of inter-population movement in each direction was classified into one of three categories, defined as follows: low = 1 black lion tamarin every ~10 years; moderate = 1 black lion tamarin every ~2.5 years; high = ~2 black lion tamarins every year, based on field observations and habitat corridor characteristics (Table 2).

Inter-population dispersal was restricted in the model to individuals between 2-4 years of age, with males (~85%) dispersing in a greater proportion than females (~15%), according to studies of the black lion tamarin (Perez-Sweeney et al., 2008) and the behaviorally similar golden lion tamarin (Kleiman and Rylands, 2008). Inter-population dispersal was achieved through probabilistic risk of dispersal for each individual age 2-4 years, with sex-biased dispersal achieved by applying a higher probability of dispersal to males than to females. Sub-adults disperse from their natal area in search of habitat and available mates; in this model, only dispersal between subpopulations is relevant and needed to be estimated.

Dispersal was limited in the model to years when population size is greater than 90% of K (N > 0.9*K) to simulate the need for

TABLE 2 Potential connectivity modeled between BLT subpopulations and habitat fragments.

#	Source subpopulation	Recipient subpopulation	Level of connectivity
1	Ponte Branca (BLT Ecological Station)	Morro do Diabo State Park (#2)	Low
		Tucano* (#18)	Moderate
2	Morro do Diabo State Park	Ponte Branca (BLT Ecological Station) (#1)	Low
3	San Maria	Agua Sumida* (#19)	Moderate
		Santa Maria (BLT Ecological Station)* (#20)	Moderate
		Santa Mônica (#4)	Low
4	Santa Mônica	Santa Maria (BLT Ecological Station)* (#20)	Moderate
		San Maria (#3)	Low
8	Paranapanema Ecological Station	Itapeva (#9)	Low
9	Itapeva	Riparian forests Apiaí-Guaçu/Taquarivaí (#11)	Low
		FLONA Capão Bonito/Apiaí-Mirim River (#12)	Low
		Buri (#10)	High
10	Buri	Riparian forests Apiaí-Guaçu/Taquarivaí (#11)	Moderate
		FLONA Capão Bonito/Apiaí-Mirim River (#12)	Moderate
		Itapeva (#9)	High
11	Riparian forests Apiaí-Guaçu/Taquarivaí	FLONA Capão Bonito/Apiaí-Mirim River (#12)	High
		Buri (#10)	Moderate
		Itapeva (#9)	Low
12	FLONA Capão Bonito/Apiaí-Mirim River	Riparian forests Apiaí-Guaçu/Taquarivaí (#11)	High
		Buri (#10)	Moderate
		Itapeva (#9)	Low
13	Angatuba Ecological Station	Riparian forests Guareí (#14)	Low
14	Riparian forests Guareí	Guareí (Santo Antônio Farm) (#15)	Moderate
		Guareí (fragment) (#16)	Moderate
		Angatuba Ecological Station (#13)	Low
15	Guareí (fragment)	Riparian forests Guareí (#14)	Moderate
		Guareí (Santo Antônio Farm) (#15)	Low
16	Guareí (Santo Antônio Farm)	Riparian forests Guareí (#14)	Moderate
		Guareí (fragment) (#16)	Low

The rate of inter-subpopulation movement in each direction was classified into one of three categories: Low = 1 BLT every ~10 years; Moderate = 1 BLT every ~2.5 years; High = ~2 BLTs every year.

* Areas where black lion tamarins are not currently present.

individuals to search areas outside of the subpopulation. Mortality (10%) was applied to dispersing animals to simulate risk of death before reaching another subpopulation. Dispersers were not allowed to enter saturated subpopulations ($N \geq K$). Individuals from adjacent areas were allowed to disperse into the three empty habitat patches included in the Pontal metapopulation (#18-20) when connectivity is estimated to exist.

Additional scenarios with no connectivity (Isolated scenarios) were run for the Alto and the Pontal metapopulations to assess the relative impact of existing connectivity on BLT population viability.

2.5.4 Initial carrying capacity

Values for K_0 for the habitat currently available to each subpopulation were estimated based on an energetic model developed with specific parameters for the species, considering the abundance of a key resource in the black lion tamarin's diet, *i.e.*, fruits of the palm Jerivá, *Syagrus romanzoffiana* (Valladares-Pádua, 1993; Passos, 1999; Mamede-Costa and Gobbi, 1998). We used information on the abundance of *S. romanzoffiana* in areas where this information was available from field studies (*i.e.*, 1-Ponte Branca/BLT Ecological Station, 2-Morro do Diabo State Park, 3-San Maria, 6-Caetetus

Ecological Station, 7-Rio Claro/Turvinho, 10-Buri, 13-Angatuba Ecological Station, 16-Guareí/Santo Antônio Farm, 18-Tucano/BLT Ecological Station, 19-Água Sumida/BLT Ecological Station) and estimated the abundance for all other areas through a simple regression between fragment size and abundance. Finally, based on these values, we estimated the carrying capacity for each subpopulation using an energetic model (Rezende et al., in prep.).

There are several methods to determine K. In this case, we used the model of nutritional contribution and energy methods (McCall et al., 1997), where the nutritional components required by the animal (dry matter, digestible energy, metabolizable energy and crude protein) are related with the kg of vegetable matter and/or the nutritional components available for animal consumption. This type of model shows a good approximation with population density and carrying capacity (McCall et al., 1997).

Considering that the Morro do Diabo population is large and believed to be self-sustaining, we assumed that the population in that area approaches carrying capacity. Based on the energetic model developed, the estimated K for this population was very close to the estimated population for this area (85%; estimated N0 = 1142, estimated K0 = 1340), which gave us confidence in using this model for estimating K for the other areas.

2.5.5 Estimated changes in K due to climate change

To incorporate the effects of climate change into K, we examined the estimates of changes in habitat suitability, based on niche models that included projections for the years 2050 and 2080 (Meyer et al., 2014), for the protected areas inhabited by BLTs in each region (Figure 1, Populations #1, 2, 18, 19, 20 in Pontal, #6 in Médio and #17 in Alto). We extrapolated these trends in habitat suitability values to the other populations in each respective region (Alto Paranapanema, Medio Paranapanema, and Pontal do Paranapanema); however, the resulting degree of change was thought by species specialists to be overestimated, with some areas losing all capacity to harbor black lion tamarins (K=0).

Colombo and Joly (2010) projected a 20% reduction of the possible occurrence of 38 plant species of the Atlantic Forest (including many genera that are key resources for black lion tamarins) due to climate change. We used this as a proxy of reduction in the carrying capacity of habitat for BLTs. Therefore, to incorporate effects of climate change into our model, we considered 20% as the maximum reduction in K that would occur by 2080 (next 60 years). We rescaled the projected losses proposed by Meyer et al. (2014) to 20% of the rates they proposed for the BLT subpopulations, following the same trend from present to 2050 to 2080. All changes were modeled as linear. For the second set of scenarios, we extended the same rate of loss from 2050 to 2080 to the end of the 100-year simulation (Table 3).

2.5.6 Risk of fire

In the model, the Catastrophe option was used to incorporate the occurrence of fires (local to each subpopulation) based on annual probabilities. The impact of fire on K and the recovery of the habitat and K were tracked through the use of custom population variables.

The Kernel Density Estimator is an interpolation technique that generates a density surface for visual identification of areas called “hotspots”, which are a concentration of events that indicates the clustering of a phenomenon in a spatial distribution. Thus, to estimate the fire risk for each fragment, a kernel map was produced using as raw data heat detection events generated and provided by the Brazilian Institute for Space Research Instituto Nacional De Pesquisas Espaciais (INPE), (2020) for the period from 2015 to 2020, within the extent of occurrence of BLTs (Figure 2). These events have, in their attribute table, a fire risk index (FRI), already calculated by INPE, using as a principle the meteorological estimate of the vegetation burning index, in which the more consecutive days without rain in a location, the greater its risk of burning. Additionally, the local effects of the vegetation type and the natural cycle of its defoliation, the maximum daily temperature and minimum relative humidity, the topographic elevation and latitude, as well as the presence of fire in the area of interest are considered in the calculation ((Instituto Nacional De Pesquisas Espaciais (INPE), 2019). These FRI values are organized into five categories, within a scale of 0 to 1: Minimum, below 0.15; Low, from 0.15 to 0.4; Medium, from 0.4 to 0.7; High, from 0.7 to 0.95; and Critical, above 0.95. For the present analysis, only those events whose FRI was equal to or greater than 0.5 were used. Therefore, we were conservative and more precise to ensure the quality of the heat detection event that was selected to produce our Kernel map.

From these selected data, we spatially modeled the distribution of known heat detection events for the years studied within our area of interest, thus observing the spatial and temporal patterns of this phenomenon. Kernel assigned a value for each pixel according to the concentration of hotspots and combined with a function that counts all points within an area of influence. Based on this value, extracted for the pixel corresponding to each record of BLT groups within a given subpopulation, we calculated the fire risk for each subpopulation - for subpopulations with more than one record, a simple average between the values was calculated. These values were then converted to annual risk of fire and added into the model as a catastrophe that results in a reduction in K, with a linear recovery of K over the length of time (Table 4). The number of years for K to return to pre-fire K considered the size and shape of the fragments (whether it is a large continuous area, smaller round/square fragment or riparian forest), since this directly influences the resilience and recovery capacity of this type of forest.

No impacts of fire on survival or reproduction were included in the model. When the population is below K, it is assumed that black lion tamarins can escape to empty adjacent (unburned) habitat in the same habitat fragment; if N is close to or at K, then reduced K in the model will cause a corresponding reduction in N due to truncation of N to K at the end of each model year.

Custom population variables were used to incorporate the interaction of fire and climate change impacts on BLT habitat (K). Vortex first calculated the estimated K for the year due to climate change. The model then applied any loss of K due to fire in that year and any habitat recovery following fires in previous fires. Finally, Vortex compared the two K values, *i.e.*, the K based on climate change (K_{CC}) and the K based on fires and recovery (K_{fire}), and used the lower value for K for that year. This prevents habitat

(K) from recovering to a level higher than the K based on climate change.

2.5.7 Catastrophic predation events

Meso-predator events (*i.e.*, brief periods of intense predation) have been observed in golden lion tamarin populations and can have a severe short-term impact in small populations (see lion tamarin PVA in Holst et al., 2006). Such events were included in this model for the six small subpopulations currently estimated with fewer than 20 individuals; for subpopulations of 20 or more individuals, predation is considered part of environmental variation. Since these events have not been observed in this species, and to be conservative, the risk used in this model was 20% of that calculated for golden lion tamarins in the 2005 PVA (*i.e.*, reduced from 10% to 2% risk of occurrence per year). This is a frequency of about once per 50 years or about 14% chance per generation. The severity of such events was modeled as a 50% reduction in survival across all sex and age classes. These values align with the default values suggested for generic severe catastrophes in wild vertebrate populations (Reed et al., 2003).

3 Results

Stochastic growth (r) was selected as the most informative measure of the sensitivity testing results. Of the ten parameters tested, all of them resulted in positive growth of at least r=0.015 over the range of values tested, suggesting that none is highly critical to model results. Age of first reproduction for females in the model (3 vs 4 years tested) was the most sensitive parameter, but this value is based on good field data and is not subject to management intervention. Other relatively sensitive parameters are the percent of adult females breeding each year, the mean number of offspring produced, and the survival rates for juveniles and subadults. Good data exist for reproduction, while survival rates are more uncertain and can be subject to various threats. Taken together, this highlights the importance of the production of surviving offspring for black lion tamarins and suggests potentially important data gaps. Adult survival also is of some, but less, influence on population growth. Maximum age (16-17 years tested) and maximum reproductive age for females (14-16 years tested) have little effect over the ranges tested and do not represent important data gaps. A generic catastrophe with default Vortex settings (50% reduction in survival, with 1.85% annual risk, based on Reed et al., 2003) has relatively little effect in large populations not under threat given the high positive growth rate. Finally, inbreeding (base values vs no inbreeding) has little impact in an initial genetically diverse population of this size and over 100 years. These results suggest that the primary area in which uncertainty may impact viability projections is for mortality rates, especially for immature individuals. This could be important if there are undetected threats that are not incorporated into the Current model scenario.

Results from the Current scenario show that, taken as a whole, the wild metapopulation of black lion tamarins is projected to retain 99.5% gene diversity and have no risk of extinction over the next 100 years under the conditions modeled, which includes projected connectivity levels. This meets the management goal for the species of retaining >98% gene diversity and having <2% probability of extinction for 100 years. However, the viability of the different BLT subpopulations varies greatly, leading to a projected loss of many smaller fragments and reduction of the species' range over time.

If we examine the viability projections for the 17 current BLT subpopulations separately, only the two large subpopulations (*i.e.*, 2-Morro do Diabo State Park in Pontal region; 17-Carlos Botelho State Park/Serra de Paranapiacaba in Alto region) meet the same viability criteria given above for long-term persistence and genetic health (Table 5). An additional three subpopulations (*i.e.*, 9-Itapeva, 10-Buri, 11-Riparian forests Apiaí-Guaçu/Taquarivaí) exhibit good viability, with at least 90% gene diversity retained and no risk of being extinct at the end of 100 years. Of the remaining 12 subpopulations, five are projected to have moderate extinction risk (~5-18%) and loss of GD (*i.e.*, 1-Ponte Branca/BLT Ecological Station, 6-Caetetus Ecological Station, 7-Rio Claro/Turvinho, 12-FLONA Capão Bonito/Apiaí-Mirim River, 13-Angatuba Ecological Station), and seven are almost certain to go extinct within 100 years (*i.e.*, 3-San Maria, 4-Santa Monica, 5-RPPN

TABLE 3 Initial carrying capacity (K_0) and climate change impacts on K after 30 (K_{CC30}) and 60 (K_{CC60}) years for each BLT subpopulation used in the Vortex model.

#	Subpopulation	K_0	K_{CC30}	K_{CC60}
1	Ponte Branca (BLT Ecological Station)	139	133	112
2	Morro do Diabo State Park	1,340	1,340	1,088
3	San Maria	63	60	51
4	Santa Mônica	60	57	48
5	RPPN Mosquito	161	129	129
6	ESEC Caetetus	204	163	163
7	Rio Claro/Turvinho	177	142	142
8	Paranapanema Ecological Station	77	74	70
9	Itapeva	176	170	160
10	Buri	270	260	246
11	Riparian forests Apiaí-Guaçu/ Taquarivaí	339	327	308
12	FLONA Capão Bonito/Apiaí-Mirim River	90	87	82
13	Angatuba Ecological Station	149	143	135
14	Riparian forests Guareí	15	14	14
15	Guareí (fragment)	17	16	15
16	Guareí (Santo Antônio Farm)	21	20	19
17	Carlos Botelho State Park/Serra de Paranapiacaba	1,314	1,346	1,275
18	Tucano (BLT Ecological Station)*	208	198	167
19	Água Sumida (BLT Ecological Station)*	128	122	102
20	Santa Maria (BLT Ecological Station)*	203	193	162

* Areas where black lion tamarins are not currently present.

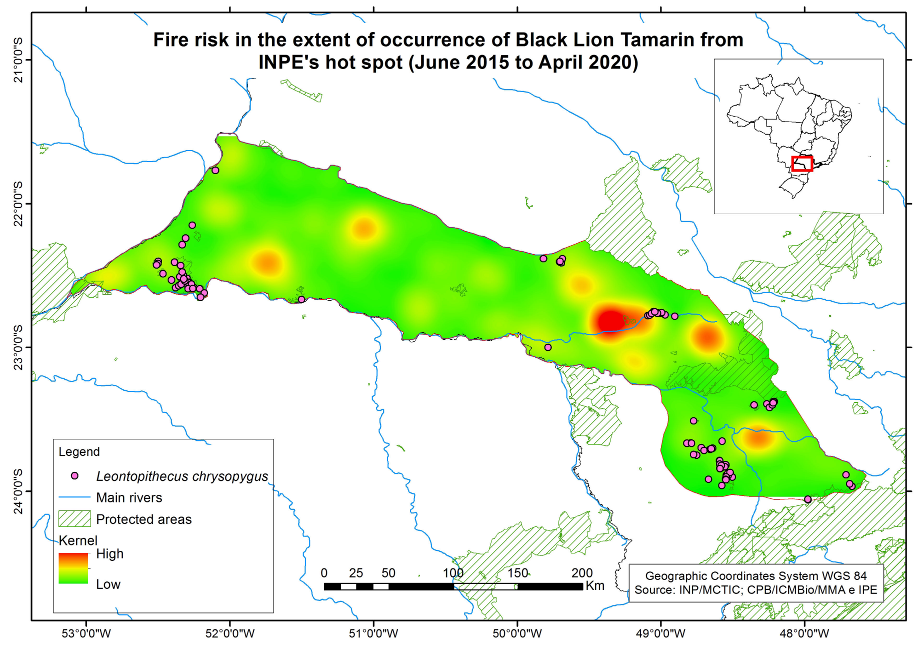

FIGURE 2
Fire risk hotspots within the extent of occurrence of black lion tamarins. Data source: INPE/MCTIC; CPB/ICMBio/MMA; IPÊ.

Mosquito, 8-Paranapanema Ecological Station, 14-Guareí/Santo Antônio Farm, 15-Riparian forests Guarei, 16-Guareí/fragment) (Figure 3; Table 5). These results suggest that, while this species may persist in the wild in core areas, many of the smaller fragmented subpopulations will disappear under the model assumptions of future threats and management, despite the possibility of recolonization through current connectivity. If survival rates are moderately lower, as explored in sensitivity

TABLE 4 Fire risk (%) and K changes for the fragments with black lion tamarin subpopulations.

#	Fragment	Initial K_0	Annual fire risk (%)	K after fire (K_{fire})	# years to return to pre-fire K
1	**Ponte Branca (BLT Ecological Station)**	139	**6.4**	132	30
2	Morro do Diabo State Park	1,340	4.0	1,313	20
3	San Maria	63	2.0	60	30
4	Santa Mônica	60	0.4	57	30
5	RPPN Mosquito	161	4.0	153	30
6	ESEC Caetetus	204	1.2	193	30
7	**Rio Claro/Turvinho**	177	**8.0**	163	50
8	Paranapanema Ecological Station	77	2.4	73	30
9	Itapeva	176	2.4	162	50
10	Buri	270	4.4	248	50
11	Riparian forests Apiaí-Guaçu/Taquarivaí	339	5.0	312	50
12	FLONA Capão Bonito/Apiaí-Mirim River	90	4.0	83	50
13	Angatuba Ecological Station	149	6.0	141	30
14	Riparian forests Guareí	15	4.8	14	50
15	Guareí (fragment)	17	4.8	16	30
16	Guareí (Santo Antônio Farm)	21	4.8	20	30

(Continued)

TABLE 4 Continued

#	Fragment	Initial K_0	Annual fire risk (%)	K after fire (K_{fire})	# years to return to pre-fire K
17	Carlos Botelho State Park/Serra de Paranapiacaba	1,314	0.6	1,288	20
18	**Tucano (BLT Ecological Station)***	208	**6.4**	198	30
19	Água Sumida (BLT Ecological Station)*	128	2.8	122	30
20	Santa Maria (BLT Ecological Station)*	203	1.6	193	30

The areas that present the greatest potential for fire risk are highlighted.
*Fragments without the presence of black lion tamarins but included in the metapopulation model.

testing, this might lower the projected viability of medium-sized subpopulations (such as #9-11) and hasten the extinction of small fragments.

The three empty habitat fragments have a low probability of recolonizing naturally given the connectivity assumptions used in the model: <4% of the iterations resulted in some recolonization for subpopulation #18, and <1% for subpopulations #19 and #20. The mean maximum population size for recolonized subpopulations was 6-7 BLTs. These recolonizations cannot be sustained in the long term (100 years) without additional immigrants, underscoring the necessity of implementing management interventions to support the persistence of these subpopulations.

Projections with no connectivity (Isolated scenarios) show the same overall long-term viability results, with large subpopulations remaining viable and the smallest subpopulations going extinct. In general, subpopulations are somewhat smaller, lose gene diversity a bit faster, and may go extinct sooner when isolated compared to the estimated low level of connectivity (Table 5).

Figure 4 shows projections for the Alto and Pontal regional metapopulations, with (Current) and without connectivity (Isolated). Both regional metapopulations show initial growth, which can be explained due to current estimated Ns being below K. For the Pontal region, current subpopulations may be below K due to stochastic events in the small populations plus three empty habitat patches, although undetected threats lowering population size cannot be ruled out. For the Alto region, early growth in the model is driven primarily by the initial low density in the large Paranapiacaba fragment (N0 = 320; K0 = 1314). The reason for the discrepancy between current estimated N and estimated K in this region is not understood and is a substantial source of uncertainty for the projected growth of this subpopulation.

Despite the initial growth of these populations toward carrying capacity in the model, these scenarios are useful to demonstrate the decline in BLT numbers over time as suitable habitat is lost through climate change and fire events. Isolation increases demographic stochasticity and inbreeding impacts, which in turn increase the likelihood that more subpopulations in small fragments will go extinct and result in lower mean population size for the species in the wild.

4 Discussion

For decades, PVA models have served as invaluable tools for evaluating species population viability and guiding conservation strategies across diverse ecosystems (Lacy, 2019). The efficacy of PVA in informing conservation decisions hinges upon the precision and validity of its underlying inputs. Accurate parameter estimation is crucial, encompassing not only species-specific biological traits and immediate threats like disease or poaching, but also factors related to habitat characteristics and associated risks. This becomes particularly vital when modeling small, isolated populations with restricted connectivity and limited prospects for expansion, as is the case with the black lion tamarin and the scenario we analyzed.

Model parameterization can be improved by utilizing diverse data sources, comprehensive and continuous field studies, and stakeholder contributions. The use of vegetative projections, energetic models and mapping of fire risk hotspots enabled us to develop an improved PVA model for wild BLT subpopulations, incorporating even climate change impacts. This model provides a baseline for testing management actions, such as conservation translocations and the establishment of forest corridors to re-establish gene flow and reduce the extinction risk of small BLT subpopulations (Valladares-Pádua, 1993; Frankham et al., 2004; Rezende, 2014).

Our results suggest the persistence of BLT core populations in the western (Pontal do Paranapanema) and eastern (Alto Paranapanema) points of the species' range, supported primarily by the two large fragments #2 and #17. Caution should be exercised, however, given the uncertainty in model inputs and assumptions. Data used for the Paranapiacaba (#17) projections in the east, in particular, include substantial uncertainty in density and carrying capacity, and field studies are required to address data gaps for this subpopulation in the Alto Paranapanema region.

The western portion of the current BLT known distribution harbor the remaining stronghold for this species. Except for Morro do Diabo State Park, all subpopulations that comprise this region are small, semi-isolated, and not viable in the long term, with projected accelerated loss of gene diversity, inbreeding accumulation, and risk of extinction. Genetic studies on the small

TABLE 5 Probability of Extinction (PE_{100}), mean population size (N_{100}), and Gene Diversity (GD_{100}) of black lion tamarin subpopulations and metapopulation at year 100, for scenarios with projected current connectivity (Current) and scenarios with no connectivity (Isolated).

#	Subpopulation	Current			Isolated		
		PE_{100}	N_{100}	GD_{100}	PE_{100}	N_{100}	GD_{100}
1	Ponte Branca (BLT Ecological Station)	0.137	26	0.800	0.191	22	0.782
2	**Morro do Diabo State Park**	**0.000**	**1,072**	**0.987**	**0.000**	**938**	**0.986**
3	San Maria	1.000	0	–	1.000	0	–
4	Santa Monica	1.000	0	–	1.000	0	–
5	RPPN Mosquito	0.891	2	0.698	0.891	2	0.698
6	Caetetus Ecological Station	0.178	45	0.832	0.178	45	0.832
7	Rio Claro/Turvinho	0.053	38	0.832	0.053	38	0.832
8	Paranapanema Ecological Station	1.000	0	–	1.000	0	–
9	**Itapeva**	**0.000**	**85**	**0.897**	**0.010**	**69**	**0.870**
10	**Buri**	**0.000**	**152**	**0.930**	**0.000**	**136**	**0.919**
11	**Riparian forests Apiaí-Guaçu/Taquarivaí**	**0.000**	**201**	**0.945**	**0.000**	**184**	**0.938**
12	FLONA Capão Bonito/Apiaí-Mirim River	0.135	25	0.825	0.701	3	0.676
13	Angatuba Ecological Station	0.068	42	0.833	0.067	38	0.824
14	Guareí (Santo Antônio Farm)	1.000	0	–	1.000	0	–
15	Riparian forests Guareí	1.000	0	–	1.000	0	–
16	Guareí (fragment)	1.000	0	–	1.000	0	–
17	**Carlos Botelho State Park/Serra de Paranapiacaba**	**0.000**	**1,278**	**0.987**	**0.000**	**1,104**	**0.986**
18	Tucano (BLT Ecological Station)	1.000	0	–	–	–	–
19	Água Sumida (BLT Ecological Station)	1.000	0	–	–	–	–
20	Santa Maria (BLT Ecological Station)	1.000	0	–	–	–	–
	Metapopulation (all fragments)	**0.000**	**2,966**	**0.995**	**0.000**	**2,576**	**0.995**

Subpopulations with good viability for 100 years (no extinction risk; ~90% GD or higher) are in boldface.

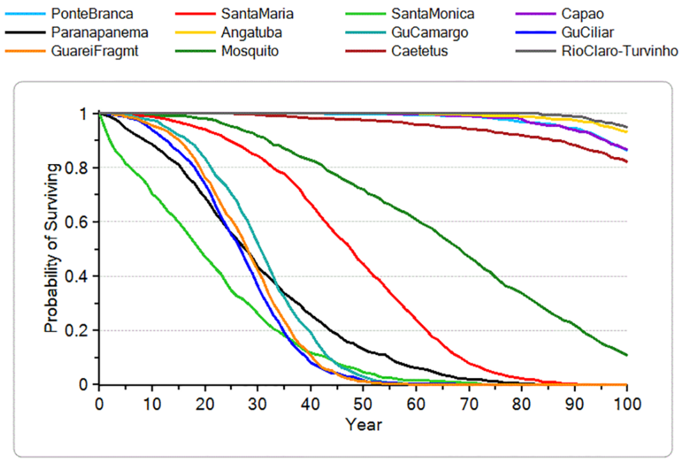

FIGURE 3
Projected mean probability of surviving over 100 years for each of the 12 current subpopulations with extinction risk >0.

subpopulations of the Pontal do Paranapanema demonstrate the importance of their conservation and long-term maintenance to preserve genetic variation, important for the metapopulation to adapt to environmental changes or pressures and, therefore, to survive (Perez-Sweeney et al., 2008). Current estimated connectivity in this region, and in the Alto Paranapanema region, is projected to be insufficient in itself to ensure long-term viability of most BLT subpopulations outside of these two large core fragments. However, to better evaluate the impact of these corridors in dispersion and recolonization processes, studies on the rate of inter-fragment movement, and the success rate (survival and reproduction) of migrants are needed.

In Pontal do Paranapanema, niche-based models project a 94% reduction of suitable habitat for the species in the Morro do Diabo State Park by 2080 (Meyer et al., 2014). We chose to use a more conservative estimate of habitat loss in this fragment for our projections, as we are unaware of the potential response and adaptation of the BLTs to these changes (Korstjens and Hillyer, 2016). Long-term studies to evaluate the impact of climate change on these primates, particularly focused on the impact of phenological shifts in food sources on the species reproductive cycle and the increased disease risk due to climate change, are indicated to provide improved parameters to the model.

Small population size is the most important factor affecting long-term viability of black lion tamarin subpopulations based on these model results. To increase population viability beyond the few larger subpopulations, it will be important to prioritize the evaluation and planning of management strategies (habitat and individuals), such as increasing protected areas, reconnecting isolated populations with corridors through forest restoration, fire prevention in areas of greatest risk, and translocations (wild-to-wild and/or captive-wild) for population supplementation aiming at increasing their genetic diversity and reducing demographic instability, such as unbalanced age structure or sex ratio. Conservation translocations may favor their adaptive potential to climate change and can be a short-term preventive action to avoid extinction while habitat connectivity is established, both strategies backed by strict forest fire control to increase their immediate and long-term chances of success. For better results in this regard, translocations must be planned and implemented considering the results from population genetic studies.

Our model indicates that restoring and reconnecting small fragments of habitat to promote the dispersal of individuals and restoring genetic flow among subpopulations can contribute to the persistence of the species across this fragmented landscape. To this end, ecological corridors are being reforested to connect small fragments to the large subpopulation of black lion tamarins found in Morro do Diabo State Park (Rezende, 2014; IPÊ, 2019). Supplementation via conservation translocation of individuals may be needed to maintain the size of these subpopulations (*i.e.*, San Maria and Santa Monica) and slow the loss of genetic diversity while these restored corridors become functional forest areas for black lion tamarins. Moreover, reintroducing the species in empty fragments subject to natural recolonization (*i.e.*, Tucano, Água Sumida, and Santa Maria, all belonging to the BLT Ecological Station) may enhance dispersal and recolonization throughout the metapopulation by conspecific attraction (Smith and Peacock, 1990; Zeigler et al., 2011). Additional modeling of such management scenarios, using this baseline PVA and informed by stakeholder input, would be valuable in developing an effective long-term BLT metapopulation management strategy.

In conclusion, this study demonstrates the importance of incorporating new data sources into a Population Viability Analysis (PVA) model of an endangered primate species, the black lion tamarin (*Leontopithecus chrysopygus*), and reinforce the importance and usefulness of such models in planning actions for its management and conservation. By enhancing the model with habitat-based inputs, such as estimates of fire risk, climate change impacts, and habitat connectivity, we have advanced the understanding of subpopulation dynamics and provided new viability projections for the species metapopulation. This work presents improved models, which resulted in critical information

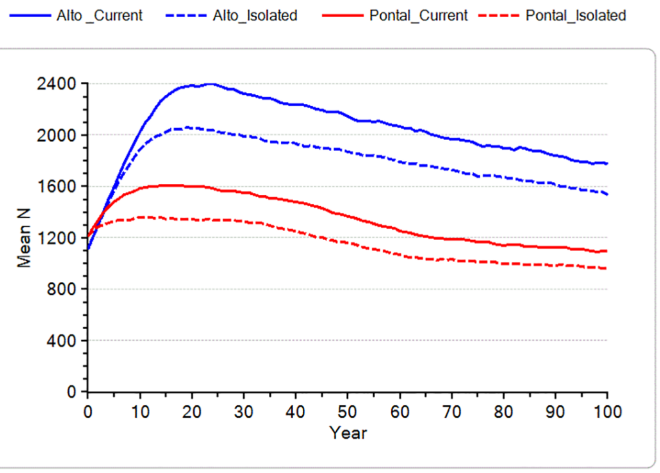

FIGURE 4
Projected mean population size for Alto and Pontal regional metapopulations, with estimated connectivity (solid) and with no connectivity between fragments (dashed).

to plan and implement conservation measures for the black lion tamarin, serving as a valuable example for how PVA can be improved for other species facing similar environmental challenges (*i.e.*, fragmentation, climate change, fires and other stochastic effects due to small population size). Thus, this research offers an innovative PVA modeling approach not only to the community focused on the conservation of lion tamarins, but also to researchers, policy makers, managers and other stakeholders involved in decision-making for species conservation.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because no data used was collected specifically for this manuscript. Data from other research or published data were used.

Author contributions

FF-S: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. GR: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. CV-P: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Validation, Writing – review & editing. FV: Data curation, Formal analysis, Methodology, Software, Visualization, Writing – review & editing. LJ: Conceptualization, Formal analysis, Methodology, Supervision, Validation, Visualization, Writing – review & editing. LP: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – review & editing. KT-H: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1423321/full#supplementary-material

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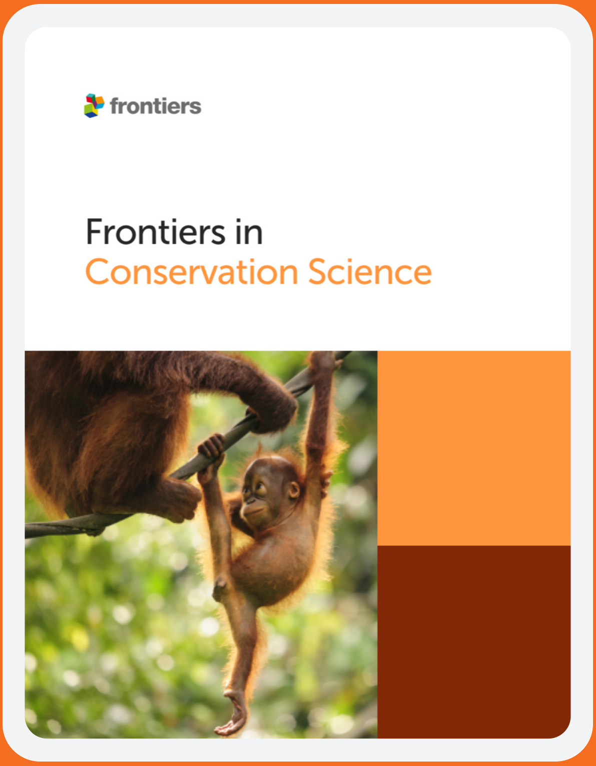

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